

Similarities and Differences in Neural Structures Involved in Echolocation in Echolocating Bats and Toothed Whales



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Abbreviations Used

Anteroventral cochlear nucleus	AVCN
Auditory cortex	AC
Constant Frequency	CF
Cochlear nucleus	CN
Columnar area of ventral nucleus of lateral lemniscus	VNLLc
Dorsal cochlear nucleus	DCN
Dorsal nucleus of lateral lemniscus	DNLL
Frequency modulation	FM
Inferior colliculus	IC
Interaural intensity difference	IID
Interaural time difference	ITD
Intermediate nucleus of lateral lemniscus	INLL
Lateral superior olive	LSO
Nuclei of lateral lemniscus	NLL
Medial geniculate nucleus	MGN
Medial nucleus of the trapezoid body	MNTB
Medial superior olive	MSO
Posteroventral cochlear nucleus	PVCN
Sinusoidal amplitude modulation	SAM
Sinusoidal frequency modulation	SFM
Superior Colliculus	SC

Abstract

Aim of this thesis is to examine possible differences in neural structures involved in echolocation caused by different ecologies of two mammalian groups. Echolocation is the process of emitting sounds and deriving information from the returning echoes to be able to navigate and forage. Bats and toothed whales possess vastly different ecologies, but have evolved sophisticated echolocation to perceive their environment.

Echolocation calls for complex processing of sounds and the integration of auditory information into the motor systems in the brain and differences in ecology may be evident in involved brain structures in echolocating bats and toothed whales. In general, the auditory system is highly enlarged, with important echolocation sound parameters overrepresented. Species with a higher dependence on echolocation often show higher hypertrophy of auditory neural structures. Some remarkable adaptations are observed in bats. The MSO, normally involved in processing ITD's in mammals, has evolved a different function in bats, most likely in prey detection and classification. The MSO in toothed whales is lacking in most species, due to the lack of detectable ITD's because of high frequency echolocation sounds and faster sound carrying properties of water. Another remarkable adaptation is the VNLLc in bats, an adaptation for exact localization of objects. Similar neural substrates have been found in the VNLL and IC of toothed whales, and they possibly possess a similar function.

The sensorimotor system also shows some remarkable adaptations according to ecology. The cerebellum is enlarged for movements in a 3D environment and, at least in toothed whales, for the rapid integration of acoustic stimuli into motor functions in the aquatic environment. Different nuclei are involved in the sensorimotor system in bats and toothed whales, which can be explained through morphological differences in sound generation and sound perception. This thesis shows differences in neural structures are evident in and between echolocating bats and toothed whales and can be related to their respective ecologies.

Introduction

Sensory modalities are shaped according to a species ecology. Animals living in low light conditions often show exceptional capabilities in sensing their surroundings by smell, touch or sound. Animals living in well-lit, open environments often have well developed vision. As form follows function, adaptations according to the prevailing sensory modality should be evident in the brain.

A remarkable case of a sensory modality taken to the extreme is hearing in the form of echolocation or biosonar. Echolocation is an active sensing system, in which an individual emits pulses of sounds and listens to the returning echoes to perceive their immediate environment. These emitted echolocation pulses bounce off objects and provide the echolocating animals with information on object location, object size and possibly even object texture and movement (Simmons et al. 1974).

Echolocation is widespread in the animal kingdom. Several (semi)-aquatic species such as California Sea Lions (*Zalophus californicianus*), harbour seals (*Phoca vitulina*), penguins (*Spheniscus humboldti*), and shrews (Soricidae) have been known to be able to use basic echolocation to forage and navigate through their surroundings. Also several flying species such as oil birds (*Steatornis caripensis*) and swiftlets and swallows (Caprimulgiformes and Apodiformes) are known to have basic echolocating capabilities (Fenton, 1984; Herzing & dos Santos, 2004). However, two groups of mammals have taken echolocation one step further: echolocating bats and toothed whales. Both of these mammalian groups heavily rely on echolocation to perceive their environment and find and catch prey items.

Bats are the most diverse mammalian group, due to the fact that they could take advantage of an unexploited niche, aerial space during the dark, through the evolution of wings and echolocation. They have highly advanced modes of echolocation, which is dependent on the species and its habitat. Most echolocating bats belong to a group called the microchiropterans that are mostly insectivorous, although some frugivorous or nectarivorous species called megachiropterans also use echolocation to navigate through their environment (Altringham, 1996).

Toothed whales, or odontocetes, have undergone extreme modifications to adapt to their aquatic environment. Their ancestors traded land for water approximately 55 to 60 million years ago and have since lost their limbs and developed elongated bodies. Due to limited use of sensory modalities such as smell and vision in water and the fact that sounds travel well through water, echolocation has evolved in toothed whales (Oelschläger et al. 2010). Approximately 67 species of toothed whales are known to use echolocation (Hof et al. 2005) to perceive their environment, and locate and catch prey (Au, 2002).

Echolocation requires remarkable feats. For example, an echolocating bat has to emit pulses of specific duration and with specific frequency and intensity components. It has to listen to the echoes and compare these with the emitted pulses, while coping with possible overlap between emitted pulses and returning echoes or noise caused by background clutter. To optimally emit pulses and receive echoes, the bat has to adjust the position of its head and pinna. The pulse repetition rate may be highly increased, for increased temporal resolution, e.g. when hunting down a prey item. Meanwhile, the animal also has to navigate through its environment, adjusting flight path according to objects or prey items (Altringham, 1996). This all requires exceptional processing of information by the brain. The brain must retrieve information from echoes to perceive the environment and this sensory information has to be relayed to motor systems to make appropriate adjustments according to the environment it is moving in. This auditory processing and sensorimotor integration has to happen rapidly in order for highly mobile animals such as bats and toothed whales to navigate through their environment, catch prey (Ulanovsky & Moss, 2008).

Echolocating bats and toothed whales have highly different ecologies. For example, they differ in body size, the medium they live in and the prey that they catch (Au, 2004). This may

reflect in their echolocating abilities. The different types of prey for example may ask for different types of echolocation to detect and recognize prey. Difference in the environment toothed whales and bats live in, i.e. water and air, can also cause differing echolocating abilities due to the different sound carrying capacities of these two media (Au, 2004).

If differences in ecology have caused different echolocating abilities, differences in brain regions involved with echolocation should be evident. Both bats and toothed whales have evolved highly evolved structures for echolocation. One of interest is the extreme hypertrophy of the auditory pathway and sensorimotor pathway (Oelschlager et al. 2010; Ulanovsky & Moss, 2008). Information obtained through echolocation needs to be processed and ultimately integrated through neural circuitry to elicit motor responses, e.g. to track prey or avoid obstacles (Valentine & Moss, 1997). Over the past 40 to 50 years, large amounts of research has been conducted (Au & Simmons, 2007) on the echolocating abilities and associated neural structures in both bats and toothed whales, showing that the auditory pathway in both mammalian groups contains highly evolved structures for echolocation. Aim of this research is to give an overview of the brain regions involved in echolocation of the auditory and sensorimotor pathway in both toothed whales and echolocating bats and try to shed light on possible differences by looking at their respective ecologies. First, a general overview on the ecologies of toothed whales and echolocating bats and their respective modes of echolocating will be given, with an emphasis on factors that could possibly influence their respective echolocation abilities. An overview of important brain regions involved in the auditory and sensorimotor systems of echolocating bats and toothed whales will be given and then we will finally discuss possible similarities and differences in echolocation and associated brain regions regarding different species of bats, different species of toothed whale and between bats and toothed whales.

Ecology and Echolocation of Bats and Toothed Whales

Echolocation allows animals to perceive objects in their environment for orientation, navigation and foraging, and is especially used by animals active in low light or low visibility environments, such as crepuscular, nocturnal or aquatic species (Herzing & dos Santos, 2004). Echolocation provides individuals with high-resolution, detailed information on position and recognition and classification of objects, e.g. prey or navigational cues in environments where sight is of little use. Retrieving information from multiple parameters from the returning echoes, e.g. frequency, amplitude and spectrum, allow for the detection, localization and classification of objects (Altringham, 1996).

The ecology of a species dictates how precise and accurate the echolocation abilities have to be. Strong selection pressure must be imposed on echolocation signal design by the echolocation tasks needed for survival. This must then drive the evolution of certain brain structures in echolocating animals. Knowing the ecology and type of echolocation used in bats and toothed whales will shed light on how and what neural adaptations in bats and toothed whales have evolved for echolocation.

ECHOLOCATING BATS

Ecology

Bats are the only mammals to have evolved active flight and evolved at least 50 millions years ago (Neuweiler, 2003). Flight and echolocation allowed this diverse group of animals to exploit a new niche, aerial space during the night, which is what made them such a successful group. Two groups of bats can be distinguished, micro- and megachiropterans. Microchiropterans are relatively small (1.5 - 150 g) and mostly insectivorous, although some species feed on larger prey items such as frogs, fish, and blood from larger mammals. Megachiropterans feed on nectar or fruit and are generally larger (20-1500 g) (Altringham, 1996).

In terms of foraging mode, aerial, gleaning and trawling bats are known. Aerial bats chase their prey in air when foraging, and are insectivores (Schnitzler et al. 2003). These aerial insectivores rely exclusively on their echolocation abilities (Denzinger et al. 2004). Gleaning bats forage from stationary objects, such as when drinking nectar from a flower or grasping prey items (e.g. insects) off the surface of e.g. leaves or ground (Schnitzler et al. 2003). These bats also use olfactory and acoustical cues produced by their prey next to echolocation to forage. Trawling species catch their prey (e.g. fish, frogs, or insects) from the surface of the water using echolocation (Denzinger et al. 2004).

Echolocating bats exist in a wide scale of habitats and the type of echolocation is well adapted to their respective habitat and prey items (Ulanovsky & Moss, 2008). Habitats are generally divided according to clutter, i.e. open area (little or no clutter), edge of forest or gaps in the forest (background clutter or intermediate clutter) and narrow space (high clutter) (Denzinger et al. 2004; Schnitzler et al. 2003). Sonar signals can differ between bats in these three different habitats in intensity, frequency and pulse repetition rate (Schnitzler & Kalko, 2001). See figure 2.1 for a representation of different habitats.

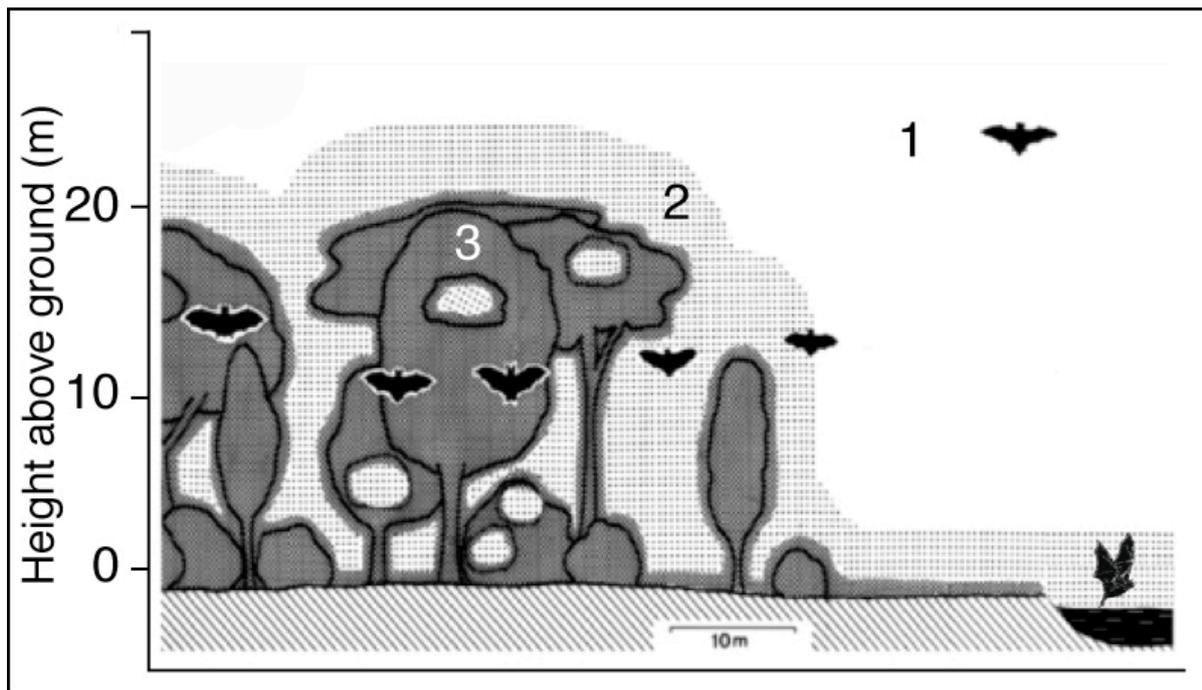


Figure 2.1. Different habitat types according to clutter. 1: Uncluttered or open space; 2. Background cluttered space or edge space; 3. Highly cluttered or narrow space. Modified from Schnitzler et al. 2003

Echolocation

Echolocation in bats is used for orientation, navigation and recognition of prey. Sonar pulses are produced in microchiropteran species by the larynx and emitted through the nose, which can be highly evolved to focus sonar pulses, or the mouth. Returning echoes are received in the ears, and pinna can be highly developed and moveable to optimally receive signals (Altringham 1996). Several species of the genus *Rousettus*, megachiropterans, emit sonar pulses not by their larynx, but by clicking their tongue (Simmons & Stein, 1980).

Echolocation calls in bats are high frequency (12 to 200 kHz) pulses. These high frequency sounds are used in echolocation, due to better object discrimination (Altringham, 1996). Pulses can be emitted at different paces, i.e. pulse repetition rates, depending on whether it is searching for prey (low repetition rate: several pulses per second) or closing in on prey (high repetition rate: up to 150 pulses per second) (Covey & Casseday, 1999). Three distinct phases have been recognized in bats during hunting. During the search phase bats display a low pulse repetition rate. After localizing a target, pulse repetition rate increases when approaching the target, and it peaks during the attack phase (See fig. 2.2B). Duration of pulses need to be shortened with higher pulse repetition rates, to prevent masking of echoes caused by outgoing pulses or background noise caused by clutter (Schnitzler & Kalko, 2001). Single or multiple pulses are emitted on each upstroke of the wings, using the energy of the wing beat to produce sound (Speakman & Racey, 1991).

Sonar signals in bats can be divided into three basic designs: frequency modulated (FM) pulses, constant frequency (CF) pulses or ultrasonic clicks (see fig. 2.2A). FM-pulses have a steep (broadband) or shallow (narrowband) down or upward sweep in frequency and can consist of several harmonics of different intensities. These sonar signals are generally short in duration (0.3-10 ms) (Au, 2004). Accurate localization of objects is made possible with broadband FM-components in sonar pulses, as they provide exact time markers for each frequency in the sweep. FM-sweeps are however less suited for the detection of weak echoes, as they do not focus a lot of energy into one frequency, and thus detection of prey. On the other hand, accurate localization is not possible with narrowband sonar signals and this type of signal is very good for detection and classification of objects, e.g. prey (Schnitzler & Kalko, 2001).

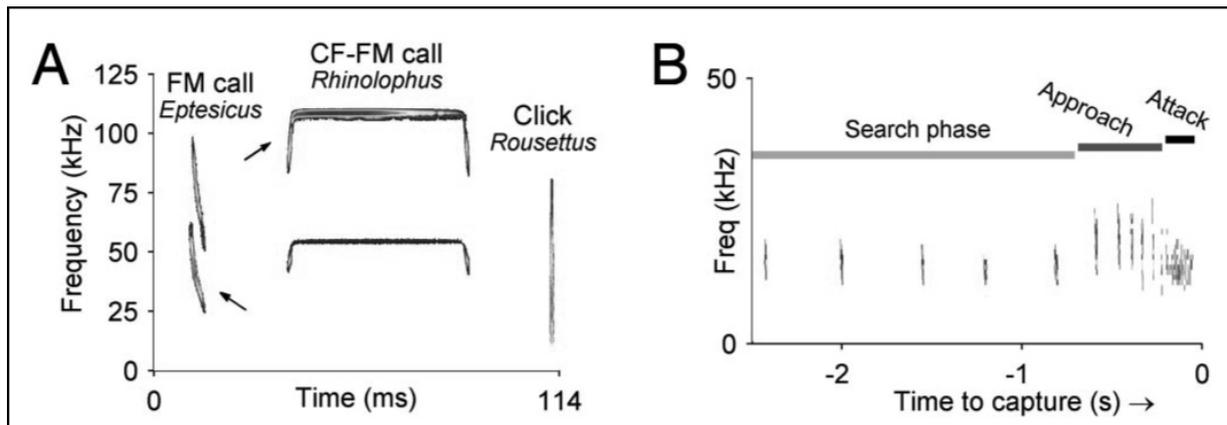


Figure 2.2. A. Audiograms of three different types of calls used by three different species of bats. On the left, a FM pulse comprising of two harmonics by the microchiropteran big brown bat (*Eptesicus fuscus*). In the middle a CF-FM pulse comprising of two harmonics by the microchiropteran lesser horseshoe bat (*Rhinolophus hipposideros*). The arrows point towards the dominant harmonics in the call. On the right the click like pulse as performed by the megachiropteran Egyptian fruit bat (*Rousettus aegyptiacus*). This shows the differences in frequency, bandwidth and duration of calls between species.

B. The pulse repetition rates during the search, approach and attack phase, showing the increase in pulse repetition rate when closing in on prey. As copied from Ulanovsky & Moss, 2008.

CF signals are of one frequency and thus narrowband and in general of long duration (10 - 300 ms) (Au, 2004). CF-pulses can consist of multiple harmonics. Long duration CF pulses allow for high performance in target detection, classification of targets and searching for moving targets in a cluttered environment (Jones & Teeling 2006). This type of pulse also allows for the use of Doppler-shift, through which speed of a bat relative to a target can be determined. With Doppler-shift, the change in frequency of the echo relative to the pulse due to movement results in accurate relative speed estimation (Schnitzler & Kalko, 2001). Most species using CF-pulses also have FM-components in their pulses for enhanced localizations of targets, e.g. CF-FM pulses (Jones & Teeling 2006).

Only several species of the genus *Rousettus* uses tongue clicks to echolocate. These clicks are of very short duration (40-50 μ s), broadband and considered rather primitive, but research has shown they are able to navigate in complete darkness very well (Holland et al. 2004).

The auditory system of the bat needs to process and analyze different temporal and spectral parameters of both emitted pulses and the associated echoes to detect, localize and classify targets. First of all, bats need to be able to distinguish their echolocation signals from other sounds, such as intraspecific communication signals, prey-generated sounds and background noise. This calls for selectivity of specific frequencies, amplitudes and durations of emitted pulses and echoes. It can also demand selectivity for e.g. specific FM-tones, and direction and rate of the FM-sweep, or specific CF tones, dependent on the species. For specific motor actions, such as changes in pulse duration according to pulse repetition rate, or change in spectrum of pulses according to echoes, selectivity for duration, frequency and modulation is also needed (Covey & Casseday, 1999; Schnitzler & Kalko, 2001; Ulanovsky & Moss, 2008).

Target localization calls for detection of azimuth, elevation and range of targets, and is performed through both monaural (input from just one ear) and binaural (input from both ears) cues. In general, mammals are able to assess azimuth, or horizontal plane, of a sound source through time differences in arrival of sound between both ears, i.e. interaural time differences (ITD's). This is however only suitable for low frequency sounds and larger animals, as the distance between the two ears needs to be sufficient to detect ITD's. ITD's are not usable for echolocating bats, as they use high frequency sounds and have relatively small heads (Grothe et al. 1992). However, horizontal position of a sound source can also be

assessed through differences in intensity between both ears, i.e. interaural intensity differences (IID's) (Pollak et al. 2002). Intensity is attenuated through air, and intensity differences arise between both ears, which is possible to detect with small interaural space and high frequency sounds. So differences in intensity and frequency need to be detected by the brain of the bat.

The pinna in bats are vital to detect elevation, or the vertical plane, of a target. Based on frequency notches, casted by the form of the ear, elevation can be detected (Wotton et al. 1996). This verifies the need to detect differences in frequency of sound sources in the brain. Target range, i.e. delay between pulse and echo, must somehow be measured in the brain by determining onset of both pulse and echo. FM bats are known to assess the delay between the onset of the first harmonic of their pulse and the onset of the echo of a higher, more intensely emitted harmonic, to assess target range. CF-FM bats assess the delay between only the first harmonic component of both the pulse and echo (Yan & Suga, 1996; Feng, 2010).

Modulations in frequency and amplitude of the echo also arise due to shape, size and movements of targets. Amplitude is dependent on target size and structure. This allows for classification of size and texture of targets in their environment by assessing notches in the spectrum of returning echoes (Sanderson & Simmons, 2000). Bats are also able to detect and classify the fluttering of insect wings through analysing sinusoidal frequency modulations (SFM) of the CF-component in the returning echo. Similar modulations in amplitude, i.e. sinusoidal amplitude modulations (SAM) are also used to extract specific features of prey (Wu & Jen, 2008). Target size can also be assessed through the duration of the returning echo. Large objects have relatively longer echoes than small objects (Firzlaff et al. 2007)

Bats using CF-components can also assess relative speed of targets, e.g. prey items, by using Doppler-shift. As a bat approaches a target, the returning echo of the CF-component will rise in frequency due to Doppler-shift. Bats compensate for this by lowering the frequency of the next pulse and this difference in frequency can be used to assess relative speed (Schnitzler & Kalko, 2001). This calls for a need to compare the emitted pulse and returning echo in frequency.

Durations of echolocation pulses are of specific lengths and can vary according to behaviour context or species. To filter out echolocation pulses, selectivity for certain durations is needed (Casseday et al. 1994; 2000; Fuzessery & Hall, 1999). Duration of pulses need to be adjusted to avoid masking of echoes by emitted pulses or background clutter, for which detection of pulse signals is also needed.

There are also many motor patterns that need to be adjusted 'on the fly' in a bat, based on the sensory input from echolocation. The use of different frequency components, harmonics, intensities, pulse durations and pulse repetition rates can vary highly according to the type of habitat or activity an individual is performing and calls for specialized control of the larynx. When closing in on a prey item, pulse repetition rate is increased. Pulse duration needs to be adjusted according to pulse repetition rate to avoid masking (Casseday et al. 1994). Different frequencies and intensities may be used as well to better localize targets. Head and pinna also need to be adjusted constantly to optimally emit pulses and receive echoes in order to detect and localize objects and prey in a 3D environment (Feng, 2010). Flight path needs to be altered according to acoustical information on obstacles and prey. All these motor patterns need to be adjusted according to the acoustical sensory system (Ulanovsky & Moss, 2008).

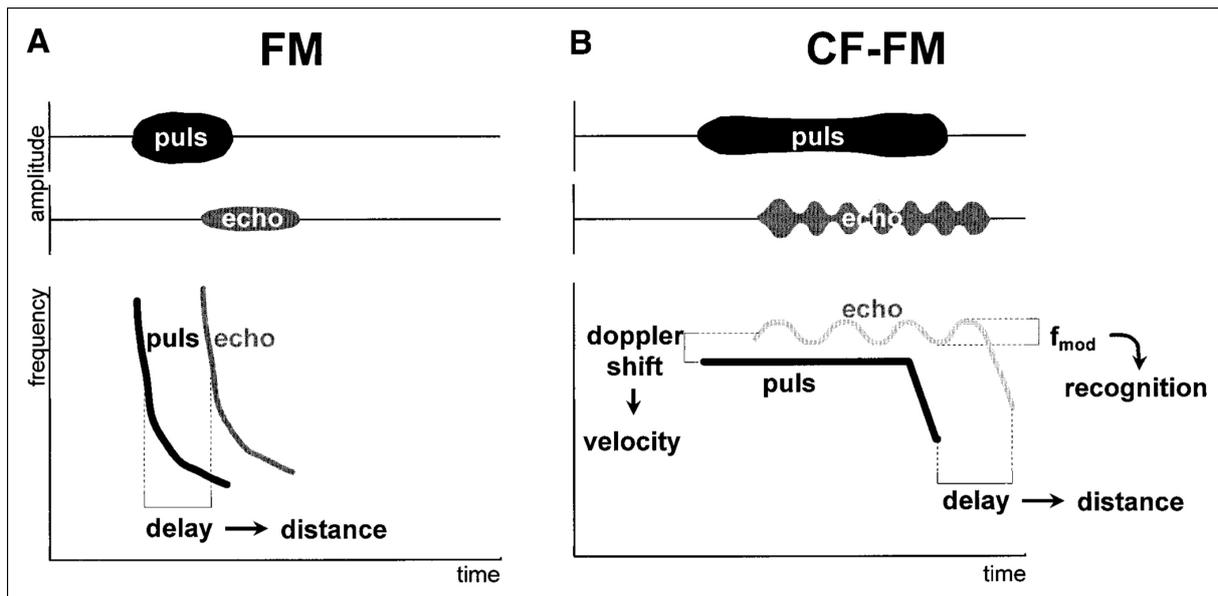


Figure 2.3 Graphs showing how amplitude and frequency components of pulses can convey certain information on prey or objects, such as distance, velocity and characteristics such as wing fluttering in FM and CF-FM bats. As copied from Grothe & Park, 2000.

TOOTHED WHALES

Ecology

Whales evolved from ungulates approximately 55-60 million years ago and have since undergone dramatic changes in body form and function (Hof et al. 2005). They have lost their limbs and evolved long spindled bodies to be able to move efficiently through the aquatic environment. They differ highly in size, from being relatively small (*Phocoena phocoena*: approximately 1.5 meter and 50 kg) to very large (*Physeter macrocephalus*: up to 16 meter and 45 tons) (Bjorge & Tolley, 2002; Whitehead, 2002). Food items generally consist of fish and squid for most species of odontocetes (Gaskin, 1982). They are known to be highly social, living in groups and may hunt in dispersed or tight school formations (Herzing & dos Santos, 2004). Communication occurs through tactile contact and low frequency sound (< 5 kHz) (Gaskin, 1982; Houser et al. 2010).

A large range of environments is inhabited, from riverine systems to open oceans. Many species are pelagic and live in the open ocean, and swim mostly close to the surface, although some are also known to dive remarkably deep. Some species are also considered semipelagic, occurring in the zone between shallow and deep water, or feeding in the open ocean, but resting at shallow inshore sites. Several species are coastal, always staying in shallow inshore sites. Some species have adapted to freshwater and are riverine (Wursig, 2002). In terms of clutter, riverine habitats have the highest amount, with mostly shallow waters and larger amounts of debris and vegetation. Inshore species and semi-pelagic species most likely also have to cope with intermediate to high amounts of clutter, while open ocean dwellers have to cope with the least amount of clutter in their acoustic environment. Other forms of clutter may not only be due to vegetation and rocks, but also due to debris in the water and even bubble screens. Type of echolocation signals used in a species depends on the habitat it lives in (Wursig, 2002; Herzing & dos Santos, 2004).

Echolocation

Echolocation in toothed whales is used to orient themselves in space, navigate and hunt for prey. Sonar pulses range are of high frequency, up to 150 kHz, and can be broad- or narrowband, with a specific peak frequency (frequency of highest intensity), that seems to

depend on body size. Large-sized species tend to have lower frequency pulses than small-sized species (Szymanski, 1999).

Sonar pulses are produced in the epicranial complex. Specialized lips originating from the nasal complex generate echolocation sounds (Cranford et al. 1996; Solntseva & Rodionov, 2007). These pulses then go through a complex sound propagating structure in the bulbous forehead, called the melon, containing air sacs and sound-conducting fats, which functions as a 'beam'-forming device to project sonar pulses as highly directional beams into the environment (Herzing & dos Santos, 2004; Au, 2002). See figure 2.4 for a representation of the epicranial complex.

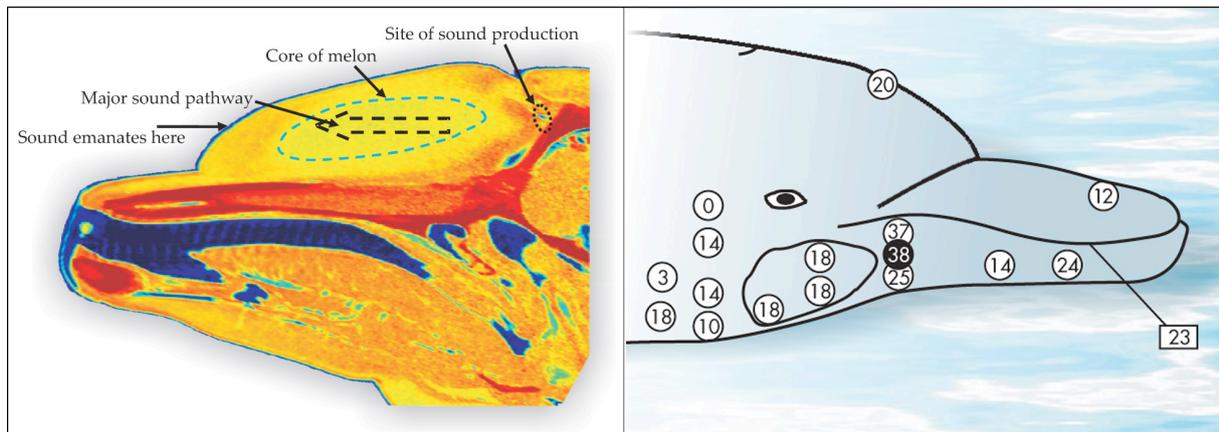


Figure 2.4. The sound generating complex of the bottlenose dolphin (*Tursiops truncatus*) is displayed on the left, showing the phonic lips, the site of sound production, and the melon. On the right different sensitivities of the jaw and head are noted, higher numbers indicating higher sensitivity. Modified from Au & Simmons, 2007

Due to similar sound of impedances of soft body tissues and water, sound reception does not actually occur through the pinna, and the external auditory system of toothed whales is but a pinhole (Au, 2002). The lower jaw has actually evolved to being sensitive for returning echoes and sound vibrations are transferred via the lower jaw to the middle and inner ears (Au, 2002). Along the jaw different frequency sensitivities have been found (see figure 2.4) and are thought to be used actively when scanning the environment (Bullock, 1968; Herzing & dos Santos, 2004).

Water carries air faster than air (approximately 4.8 times) and has very low absorption of sound, probably explaining why echolocation signals of odontocetes are of very short duration, which allows for distinguishing pulse from echo, and high intensity (Herzing & dos Santos, 2004). Echolocation pulses between species differ in structure, intensity, frequency and pulse repetition rate (Herzing & dos Santos, 2004). These echolocation pulses are also known as clicks and can be divided into two main groups. Whistlers, with broadband and short (<100 μ s) clicks, and non-whistlers, with narrowband and long (>125 μ s) clicks (Herzing & dos Santos, 2004; Au, 2004). See figure 2.5 for the differences in audiogram for the two groups.

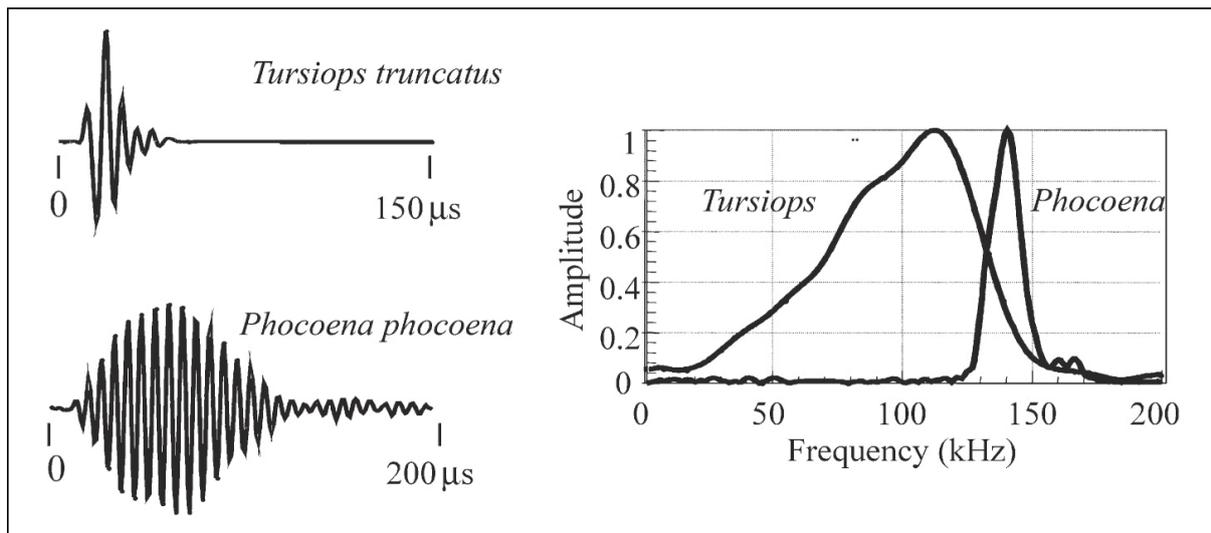


Figure 2.5. Echolocation pulses of a bottlenose dolphin (*T. truncatus*) and a harbour porpoise (*P. phocoena*) showing the differences in duration, bandwidth and peak frequency between a whistler and a non-whistler. Copied from Mooney et al. 2007

Another distinction between whistlers and non-whistlers can be made according to sociality and environment of species. Whistlers are generally speaking species with highly social lives, which use low frequency communication signals, such as most species of dolphins and some species of porpoises. Non-whistlers are mostly inshore porpoise, some smaller dolphin species and riverine species, which live in more turbid waters and thus need higher performance in echolocation perception (Herzing & dos Santos, 2004).

Due to the similar sound impedances of water and body tissues, toothed whales can actually look 'inside' their prey. Internal composition of fish can thus be distinguished and aids in the discrimination of different fish species (Herzing & dos Santos, 2004).

Spectral and temporal features of echoes need to be processed in the odontocetes brain, although little is known on what sound parameters are used by toothed whales and how they adjust their echolocation pulse to different behavioural or environmental contexts (Matsuo et al. 2009; Ibsen et al. 2010). However, filtering of certain temporal and spectral parameters must occur in order for them to perceive their environment and prey as they do (Au et al. 2009).

Despite the relatively large size of toothed whales, object localization in the horizontal plane most likely does not occur via ITD's due to the high speed at which sound travels through water, causing minute, non-detectable ITD's. IID's are more likely used for object localization when using high frequency, echolocation pulses, although ITD's may also be used for low-frequency sounds (Herzing & dos Santos, 2004). For localization in the vertical plane, different sensitivities of the jaw are most likely used to detect spectral differences (Herzing & dos Santos, 2004). Target distance is measured by echo delay, as is done in bats (Au et al. 1988).

Using notches in spectra's of echoes and specific modulations of frequency are most likely used to assess sizes and shapes of objects in the immediate environment. In specific prey recognition, variation in amplitude and overall duration of echoes are used. Differences in amplitude and duration of echoes are caused by shape and inner structure of the fish, and have also been shown to depend on the angle at which it is perceived (Au et al. 2009). Dolphins have been observed swaying their head side to side when investigating prey in the sand, and this may provide specific amplitude and frequency modulations similar to the SFM and SAM that bats use to categorize prey (Herzing & dos Santos, 2004). Prey may also be identified by processing change in echo amplitude, timing and echo structure from subsequent pulses (Au et al. 2009). So it is likely specific frequency and amplitude modulations are highly important for analyzing prey in toothed whales. However, aquatic

echolocating animals cannot use Doppler-shift. Sound travels too fast through water to actually perceive relevant changes in speed through Doppler-shift (Herzing & dos Santos, 2004).

Many motor actions need to be adjusted accordingly while echolocating in toothed whales. Increase in pulse repetition rate is observed when approaching prey, the pulse beam has to be aimed in specific directions and possible changes in features of pulses may occur according to the situation. This must demand high control of the phonic lips and melon (Au et al. 2009; Ibsen et al. 2010). Change in head and swimming direction are also used to aim pulses and to optimally receive echoes (Herzing & dos Santos, 2004). Echoes are also likely to provide feedback control on click production (Ibsen et al. 2010). It is clear that in toothed whales, the auditory information derived from echoes must be integrated with the motor systems.

Neural Adaptations in Regard to Echolocation

Research over the past four decades has shown that in general, the brain in echolocating bats and toothed whales have the same blueprint as all other mammals, albeit with several remarkable adaptations (Marino et al. 2001; Covey, 2005). Winer and Larue (1996) suggest that due to found conservancy in structure of the nervous system in multiple mammalian species, differences will largely be evident in size and elaboration of nuclei.

I will first give a brief review of the major brain structures involved in the central auditory system and several accompanying sensorimotor pathways relevant to hearing in the 'standard mammalian brain' and their respective functions. Then I will discuss all the major brain structures that have been adapted for echolocation through evolution in both echolocating bats and toothed whales.

AUDITORY SYSTEM AND ASSOCIATED MOTOR SYSTEMS OF THE MAMMALIAN BRAIN

The peripheral auditory system accounts for the conversion of sound into neural information, which can then be further transmitted to multiple regions in the brain (Sachs & Blackburn. 1991). Sound is generally picked up by the pinna, the external ear structures, and transferred to the cochlea via the tympanic membrane and middle ear to the inner ear, where the sound signals are converted into spike discharges (Purves et al. 2004).

From here on it is called the central auditory pathway. The spike discharges from either ear are carried by the auditory nerve to the cochlear nuclei (CN) located in the brainstem. The auditory nerve branches and provides input into three portions of the CN, the anteroventral central nucleus (AVCN), posteroventral cochlear nucleus (PVCN) and the dorsal cochlear nucleus (DCN). The auditory nerve can already be selective for species-specific sounds, eliminating noise being carried through to the central auditory system. Neural information is carried from the CN to the superior olivary complex (SOC) and the nuclei of the lateral lemniscus (NLL) (Purves et al. 2004).

The SOC comprises of three important nuclei: the medial superior olive (MSO), the lateral superior olive (LSO) and the medial nucleus of the trapezoid body (MNTB). The SOC is part of the binaural pathway, i.e. neurons of the SOC receive input from the AVCN's of both ears, and are thus important for the horizontal localization of sound. The MSO processes ITD's of low frequency sounds to assess azimuth (Purves et al. 2004). As these time differences are too small to assess in species with small heads or that use high frequency sounds, these species often lack an MSO (Grothe et al. 1992). The LSO and MNTB work in conjunction to deal with IID's of higher frequency sounds, of which ITD's cannot be sensed, and localize horizontal positions of sound sources through differences in intensity between the two ears. The nuclei of the lateral lemniscus (NLL) consist of three nuclei: the ventral, intermediate and dorsal nucleus of lateral lemniscus (VNLL, INLL and DNLL, respectively) (Covey & Casseday, 1999). It receives projections from the CN as well as the SOC. The NLL belongs to the monaural pathway, i.e. neurons of the NLL receive input from CN or SOC of either hemisphere. It is involved in processing temporal aspects of sound, e.g. onset of sound stimuli (Purves et al. 2004).

All auditory nuclei of the brainstem (CN, SOC and NLL) converge in the inferior colliculus (IC) in the midbrain. It is an integration centre for all auditory processing of lower brainstem nuclei and also provides an additional processing centre, before auditory input is further relayed to the auditory thalamus and auditory cortex. The IC is able to process sounds with complex temporal patterns, such as frequency-modulated sounds and sounds of specific durations (Purves et al. 2004).

The IC provides the medial geniculate nucleus (MGN) in the auditory thalamus with inputs of spectral and temporal pathways, which aids the MGN in detecting specific spectral and temporal combinations of sounds, e.g. combinations of specific FM sweeps of different

harmonics. Although most input to the MGN is from the IC, it receives some input from lower brainstem nuclei as well (Purves et al. 2004).

The auditory thalamus projects to the auditory cortex, which in most mammals is located in the temporal gyrus of the temporal lobe. It is highly tonotopic and is involved in higher order processing of natural sounds. It can be highly modular to assess different temporal and

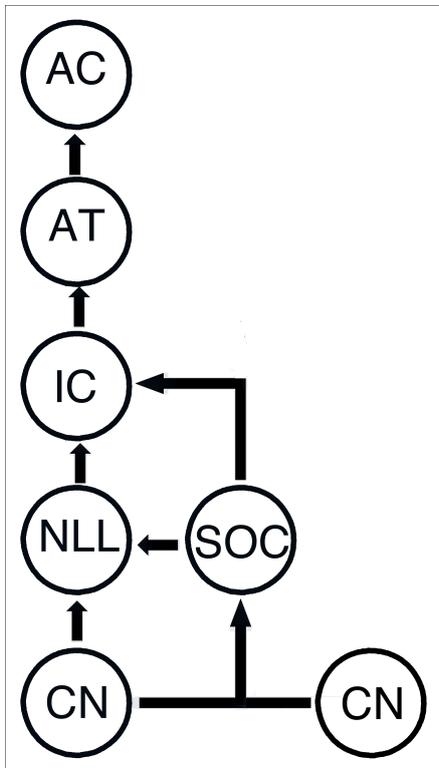


Figure 3.1 Representation of the auditory pathway. The SOC receives input from both ears, while the other brainstem nuclei in general receive input from either ear.

spectral aspects of sound, depending on auditory information that is critical for a species survival (Purves et al. 2004). See figure 3.1 for a simplified representation of the auditory pathway.

Several brain regions are also associated with motor responses. Only the ones relevant to echolocation will be discussed. The cerebellum is very important in coordinating movements, and for balance and posture. Neural information from the cerebral cortex is relayed to the cerebellum via several nuclei in the medulla and pons (Purves et al. 2004; Oelschlager et al. 2010), which is then further relayed towards the cerebellum. The superior colliculus (SC) is associated with orienting behaviours, such as eye saccades and head movements and is located in the midbrain. The facial nucleus is located in the brainstem and is associated with the control of superficial facial muscles, as well as vocalization and mastication (Oelschlager et al. 2010). It innervates the muscles associated with these actions via the facial nerve. The trigeminal nerve innervates sensory information from the face and body and also activates the muscles associated with mastication (Purves et al. 2004)

BATS: NEURAL STRUCTURES AFFECTED BY ECHOLOCATION

Bats show an overall enlargement of brain regions involved in the auditory system and also in several regions of sensorimotor pathways. Due to enlargement of auditory nuclei in the brainstem, these nuclei comprise of approximately 14-23% of the brainstem in echolocating bats, compared to only 5.3-8.5% in non-echolocating bats, indicating a highly specialized brainstem for echolocation (Hu et al. 2006). The midbrain, with the inferior colliculus and the auditory thalamus, is also enlarged and highly specialized (Covey, 2005). The auditory cortex in echolocating bats is the largest of all sensory cortices, often with high modularity to specific tones associated with echolocation pulses and echoes (Suga et al. 1978; Mittmann & Wenstrup, 1995; Yan & Suga, 1996; Vater et al. 2010; Macias et al. 2009; Razak & Fuzessery, 2009; Feng, 2010). The major nuclei of the ascending auditory pathway will be discussed, as well as several sensorimotor nuclei that have been found to be important in echolocating bats.

Auditory System

Cochlear Nucleus

The cochlear nucleus in echolocating bats is not structurally different from those in other mammals (Haplea et al. 1994; Covey & Casseday 1995, Covey, 2005). It has similar tonotopic representations as found in e.g. cats (Covey & Casseday, 1995). The CN in echolocating bats can be considered large relative to brain stem volume (Covey & Casseday,

1995). The auditory nerve is enlarged as well. Biologically relevant sounds, i.e. high frequency sounds, are overrepresented and form an acoustic fovea of important frequencies in the CN (Kossl, 1994; Vater & Kossl 2010). In bats using an FM-component in their echolocation pulses, this fovea represents the range of frequencies in their FM sweep. In bats using a CF-component in their pulses, the CN displays narrow frequency tuning to the CF frequency (Haplea et al. 1994; Covey & Casseday 1995; Marsh et al. 2006).

The AVCN is enlarged and well developed, and can form up to half of the entire CN in some species of echolocating bats. It is developed to process the high frequency sounds used in sonar signals (Covey & Casseday 1995). The PVCN is very similar in structure compared to other mammalian species. One striking feature is that it does have significant projections to the IC (Covey & Casseday, 1995). The DCN is, in contrast to the AVCN and PVCN, hypotrophied and small compared to the DCN in other mammals. It also does not display distinct lamination, which is the case in most mammals (Covey & Casseday, 1995).

Superior Olivary Complex

Like the CN, the SOC is enlarged and very well developed in echolocating bats. It comprise of the same three nuclei as in other mammals, the LSO, MSO and MNTB. All structures are large in comparison to the brainstem (Covey & Casseday, 1995).

The LSO and MNTB are very similar in structure to other mammals (Covey & Casseday, 1995), and most likely functions in processing IID's. The MNTB is a very prominent feature of the SOC (Grothe et al. 1992; Grothe & Park, 2000). It projects to several nuclei of the SOC, the INLL and VNLL (Covey & Casseday, 1995) and is associated with high frequency regions of the VCN, MSO and LSO (Yavuzoglu et al. 2010), indicating its use in processing of echolocation signals.

The MSO is the most modified structure of the SOC. It seems to be different in comparison to the MSO of other mammals, possessing monaural neurons as well as binaural neurons, (Grothe et al. 1997; 2001) and does not seem to necessarily process ITD's, but other temporal patterns of echoes. Its function seems to lie in pattern recognition, e.g. specific frequency or amplitude modulations by prey, of echo parameters (Grothe & Park, 2000).

Differences in MSO size and anatomy exist between different species of bats and seem to be related to echolocation call design. In most species, it displays frequency tuning according to the species audiogram. Respective frequencies important to a species, i.e. best frequency, are overrepresented (Grothe et al. 1997; Grothe & Park 2000). FM bats do not have neurons sensitive to pure tones (Grothe, 2000) and have as many binaural neurons as other mammals, i.e. a mostly binaural MSO (Grothe et al. 1997; Grothe & Park, 2000; Grothe, 2000; Grothe et al. 2001). Bats using CF-components in their pulse have an extremely enlarged and mostly monaural MSO (Grothe & Park 2000; Grothe et al. 2001). Species that use pseudo-CF-components in their pulses, i.e. very shallow FM sweeps of long duration, seem to have an MSO in between CF bats and FM bats in anatomy and size (Grothe et al. 2001). This indicates the MSO is highly adapted to species-specific pulse components. See figure 3.2 for a comparison of SOC nuclei in three different mammalian species.

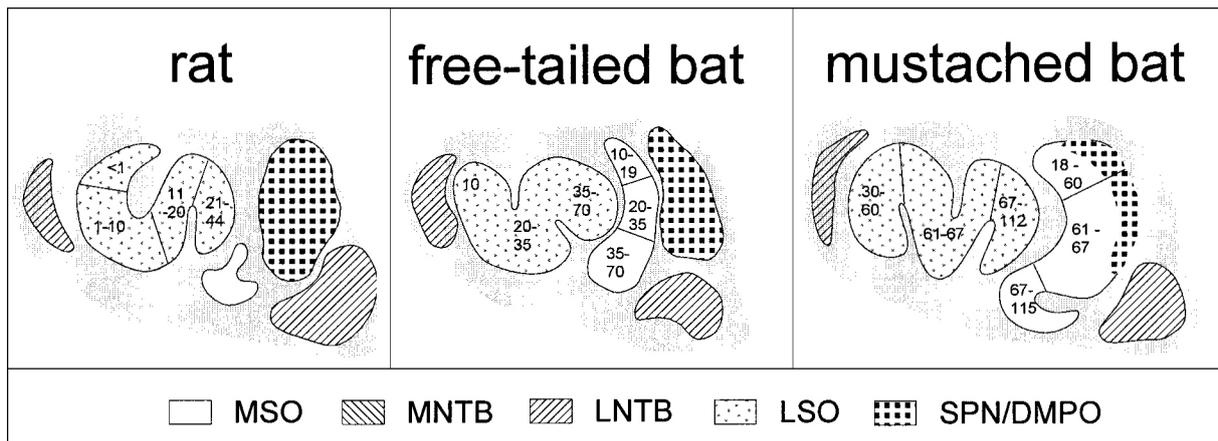


Figure 3.2. Outline of the principle SOC nuclei in three different 'high-frequency hearing' mammals (Rat, *Rattus norvegicus*; Mexican free-tailed bat, *Tadarida brasiliensis*; mustached bat, *Pteronotus parnelli*), showing the different arrangements of the medial regions. Note that the tonotopic arrangement is similar in all three species and the size difference of the MSO between the three species. The mustached bat, a CF-FM bat, clearly has a larger MSO than the free-tailed bat, a FM-bat. Modified from Grothe & Park, 2000

Nuclei of Lateral Lemniscus

The lateral lemniscus comprises of three nuclei, the VNLL, INLL and DNLL (Covey & Casseday, 1995). Although the DNLL is similar in size and structure to those found in other mammals (Covey & Casseday, 1986), the VNLL and INLL in echolocating bats are greatly enlarged, show a high degree of differentiation and provide a major input to the IC (Covey & Casseday, 1991; Covey, 2005). These nuclei can also differ between species (see figure 3.3), although this is thought to be more related to phylogeny than echolocation pulse design (Covey, 2005). The NLL are thought to process different frequencies or temporal parameters in a parallel fashion, relaying the different aspects of different parameters to higher order brain structures (Covey & Casseday, 1991).

The VNLL can be subdivided into two separate areas, the multipolar cell area (VNLLm) and the columnar area (VNLLc), which is the most striking region (Covey & Casseday, 1986). The VNLLc is highly tonotopically organised, with broad frequency tuning and all audible frequencies represented dorsoventrally (Haplea et al. 1994). Frequencies relevant to echolocation are overrepresented (Covey & Casseday, 1986). It is thought the VNLLc acts as a frequency funnel, sending certain frequency parameters to different areas of the IC (Covey & Casseday, 1986).

The INLL is highly enlarged. It has combination-sensitive neurons, which combine temporal and spectral cues. Sensitivities for combinations of specific harmonics of calls have been found (Portfors & Wenstrup, 2001). These are further projected to combination-sensitive neurons in the IC.

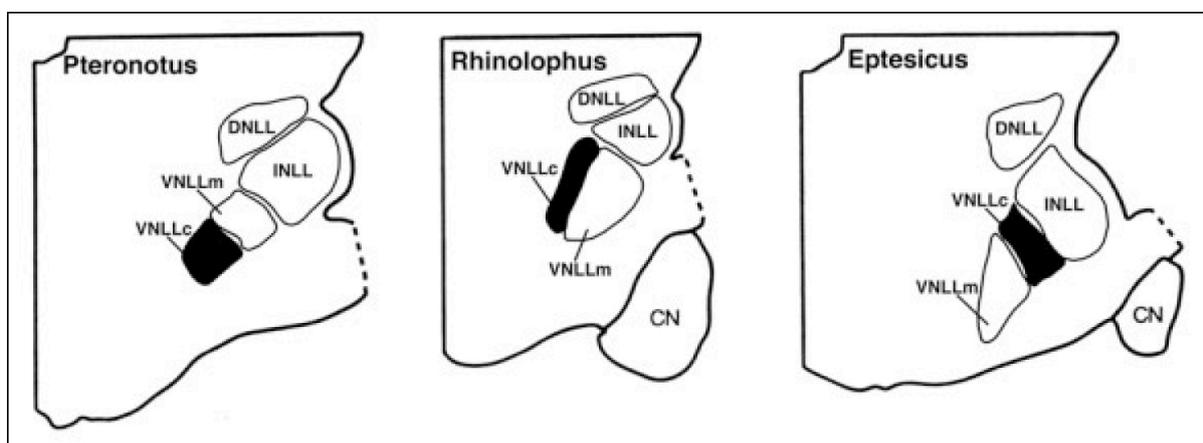


Figure 3.3. Nuclei of the lateral lemniscus of three species of bats; *Pteronotus* (a CF-FM bat), *Rhinolophus* (a CF-FM bat) and *Eptesicus* (a FM bat). The DNLL is very similar in all species, but the more ventral nuclei are variable, especially the VNLLc (shaded). Adapted from Covey, 2005

Inferior Colliculus

The IC is highly enlarged and found to be five to six times and three to four times as large in echolocating microchiropterans and echolocating megachiropterans respectively, compared to non-echolocating megachiropterans (Hu et al. 2006). The IC is where many fibres from different nuclei innervate and is a major processing centre of auditory information (Pollak & Park, 1995; Covey et al. 1996). It has large projections to the MGN in the auditory thalamus, smaller projections to the SC and provides feedback to lower nuclei such as the LSO and the CN (Pollak & Park, 1995).

It is very strongly tonotopically organised in various sheets of frequency bands, but with much narrower frequency tuning than in the NLL (Pollak & Park, 1995; Haplea et al. 1994). It can be divided into three distinct regions; a ventral region that is tuned to biosonar frequencies and a lateral and dorsal region, that are both tuned to the lower frequency spectrum of the bats audible range (Fuzessery & Hall, 1999). The dorsal and lateral region are possibly a species-specific adaptation to process sounds obtained through passive listening, e.g. in gleaning bats using prey-generated sounds to detect prey (Fuzessery & Hall, 1999).

In bats using CF-components, the ventral region has a strong overrepresentation of the used CF frequency, most likely to do with detection of fluttering insects by analyzing echo frequency modulations caused by the insect's wing beats (Goto, 2010) and detecting Doppler-shift. In FM bats the best frequencies of the FM-component of their pulse is also overrepresented, although not as strong as in CF-bats. Some FM bats have a quasi-CF-component at the end of their pulse. In these species this frequency is also overrepresented in the IC (Goto, 2010). See figure 3.4 for a tonotopic representations of the IC's of three different bat species.

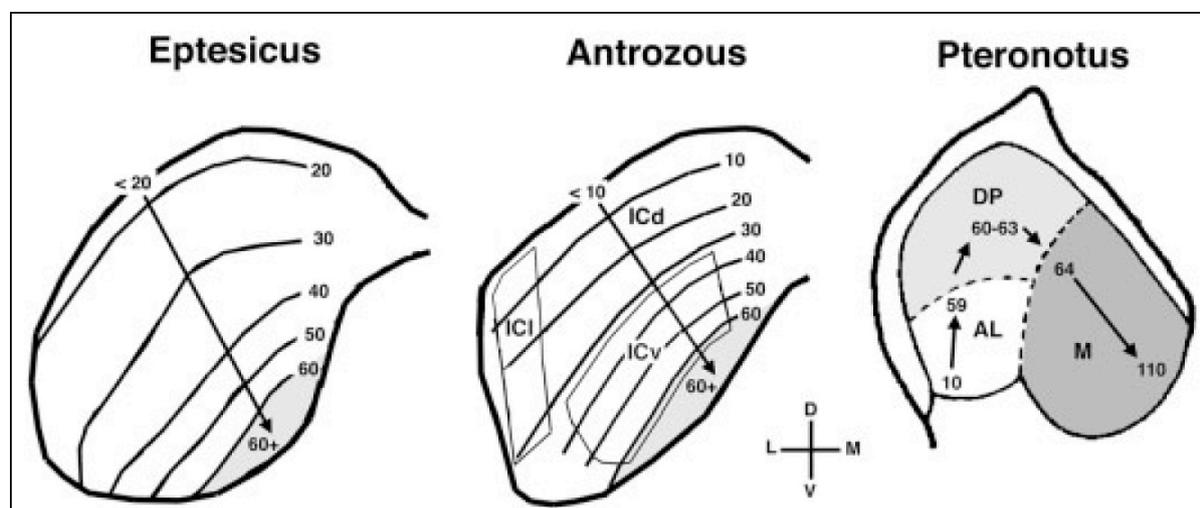


Figure 3.4 Different tonotopic representations in the IC of three species of bats (the big brown bat, *Eptesicus fuscus*, a FM-bat; the pallid bat, *Antrozous pallidus*, a FM-bat that also used prey generated sounds to detect prey; and the mustached bat, *Pteronotus parnelli*, a CF-FM bat). The numbers represent the frequency sensitivity in kHz. White and grey areas represent frequencies below and above 60 kHz respectively. In *Pteronotus*, the light grey shade area represents the acoustic fovea, which is tuned to 60-63 kHz, and the dark grey area represents frequencies above 63 kHz. AL: anterolateral region of IC; DP: dorsal posterior region of IC; M: Medial region of IC; ICl: Lateral region of IC; ICv: ventral region of IC; ICd: dorsal region of IC. Arrows indicate the tonotopic axis from low to high frequency. Copied from Covey, 2005

There are many other types of neurons in the IC that are tuned to distinct relevant echolocation pulse parameters, such as neurons tuned to sound duration (Casseday et al.

1994; 2000: Covey et al. 1996; Faure et al. 2003; Feng 2010; Fremouw et al. 2005; Fuzessery & Hall 1999; Luo et al. 2008), pure tones (Casseday et al. 1994), FM sweeps of pulses (Casseday et al. 1994, 1997; Fuzessery et al. 2006; William & Fuzessery, 2010), SAM (Covey et al. 1996; Casseday et al. 1997), SFM (Casseday et al. 1997), combinations of different harmonic components of pulses (Wenstrup et al. 1999; Mittmann & Wenstrup, 1995) and to Doppler-shifts (Pollak & Park, 1995). Exact details of these selectivities of neurons are likely to be species-specific (Fuzessery et al. 2006).

The IC is the first place where duration-sensitive neurons are found. (Casseday et al. 1994; Fuzessery & Hall, 1999; Casseday et al. 2000; Faure et al. 2003; Fremouw et al. 2005; Luo et al. 2008). In the different species where these neurons have been found, they are tuned to the length of relevant calls, i.e. the length of their respective echolocation pulses (Luo et al. 2008). Duration-sensitive neurons dependent on certain intensities can exist in the bat's IC, and are likely functioning in echolocation. Pulse and echo differ in intensity, and can be divided into two different information streams by duration-sensitive neurons with different intensity, but similar duration preferences, allowing for comparison of echo and pulse (Fremouw et al. 2005). This theory is further supported by the fact that these duration-sensitive neurons are found more in areas with frequencies corresponding to the CF-component or FM-component of a species' echolocation call (Fremouw et al. 2005; Wu & Jen, 2008).

Delay-sensitive neurons have also been found in the IC of bats. Paradoxical-latency-shift (PLS) neurons seem particularly important, which can account for the weaker intensity of a returning echo, compared to the emitted pulse, to encode delay. Some species-specific differences in amount of PLS neurons in the IC may exist, with lower percentages of PLS neurons in FM-bats (10% in big brown bats, *E. fuscus*: Ma & Suga, 2008; 13% in Mexican free-tailed bats, *T. brasiliensis*: Klug et al. 2000) than CF-FM bats (29% in little brown bats, *Myotis lucifugus*: Galazyuk & Feng, 2001).

Neurons tuned to pure tones and FM sweeps are likely to be important in detecting certain or different components of pulses (Casseday et al. 1994). Selectivity for direction of sweep, i.e. up or down modulated, steepness or rate of the sweep, and duration of tones or sweeps have been found (Casseday et al. 1994; 1997; Fuzessery et al. 2006; William & Fuzessery, 2010).

Combination-sensitive neurons such as FM/FM-neurons are the most well known in the bats IC. These neurons integrate information from the first harmonic of the emitted pulse and a higher harmonic of the returning echo to encode target distance (Mittmann & Wenstrup, 1995).

Neurons sensitive to sinusoidal frequency or amplitude modulations (SFM and SAM) also exist in the bat's IC (Covey et al. 1996; Casseday et al. 1997). These neurons detect spectral temporal patterns in the bat's echo and are exceptionally important for detecting wing fluttering of insects, which causes these sinusoidal modulations.

Auditory Thalamus

The auditory thalamus controls the flow of information towards the cortex, in which the MGN is particularly important. Its importance in echolocation has been derived from its number of GABAergic neurons in one study (Winer & Larue, 1996), of which it had very few compared to several other mammalian species. This difference was not noted in the lateral geniculate body, which belongs to the visual system. Thus, the low number of GABAergic neurons is a species-specific arrangement (Winer & Larue, 1996), and must be a specialization for echolocation in bats.

The MGN displays sharp tuning to a tonotopic map, sharper than collicular neurons in this respect, and thus processing of target distance is superior in the MGN than in the IC (Yan & Suga 1996). It also possesses combination-sensitive neurons. Again, these combination-sensitive neurons show specific frequency tuning to harmonic components of pulses, encoding target distance (Mittmann & Wenstrup, 1995; Winer & Larue, 1996).

Auditory Cortex

The auditory cortex is larger than all other sensory cortices and highly specialized for distinct components of echolocation pulses.. It receives its major input from the MGN in the auditory thalamus and provides feedback to the nuclei in the midbrain (Xiao & Suga, 2002; Mittmann & Wenstrup, 1995). It is believed the AC has better information processing capabilities than the MGN and especially the IC (Yan & Suga, 1996). All species show tonotopic maps, but only CF-FM bats have overrepresentations of specific echolocation pulse frequencies, i.e. the CF-component. In FM-bats, this has only been shown in one species (Macias et al. 2009). See figure 3.5 for a comparison in tonotopic representations in the AC between two species of bats. These frequency-tuned neurons also have high minimum intensity threshold, showing they are specifically used for processing of loud echolocation pulses (Macias et al. 2009). In most species it shows very high modularity, with distinct areas of the AC tuned to echo delay, frequency sweeps (sensitive for rate and direction), specific frequencies (e.g. CF-component of pulses) or Doppler-shift (Suga et al. 1978; Mittmann & Wenstrup, 1995; Yan & Suga, 1996; Vater et al. 2010; Macias et al. 2009; Razak & Fuzessery, 2009; Feng, 2010).

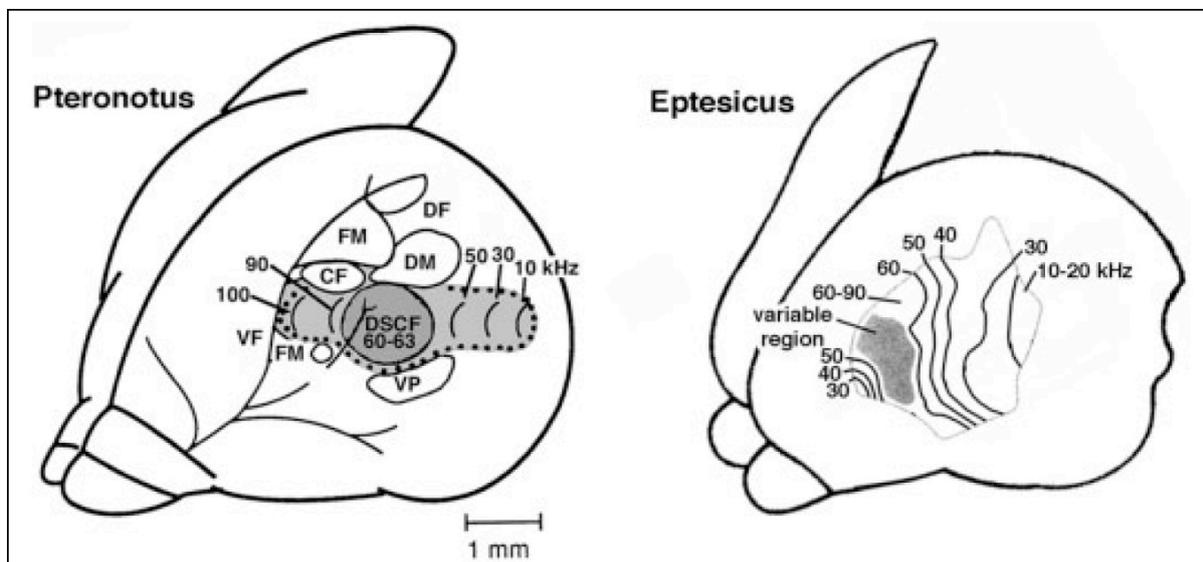


Figure 3.5 Auditory cortical organization of two species of bat, *Pteronotus parnelli*, a CF-FM bat, and *Eptesicus fuscus*, a FM bat. The shaded area in *Eptesicus* indicates a region that is highly variable across individuals. Abbreviations used are CF, combination-sensitive CF-CF area; DF, dorsal fringe area; DM, dorsomedial area; DSCF, Doppler-shifted CF2 area or auditory foveal representation; FM, delay-sensitive FM-FM area; VF, ventral fringe area; VP ventral posterior area. Copied from Covey, 2005

Sensorimotor System

Cerebellum and Associated Nuclei

Nuclei in the pontine grey receive a large projection from the IC (Covey, 2005), which projects to the enlarged cerebellum in echolocating bats (Marino et al. 2000). This IC-pontine-grey-cerebellum pathway is thought to be a specialization for enhanced motor control in the 3D environment bats move in (Covey, 2005).

Superior Colliculus

The SC is involved in orienting behaviours (Sinha & Moss, 2007). In the case of the bat this does not only involve moving of the head and pinna, but also the aiming and emittance of echolocation pulses (Valentine et al. 2002). Relative size of the SC does not differ between mega- and microchiropterans (Hu et al. 2006). There is however only little auditory input to the SC in megachiropterans (Thiele et al. 1996). In microchiropterans, the outer layer, which is linked to the visual system, is only thin (Sinha & Moss, 2007). Many auditory neurons are

however found in the deeper layers (Thiele et al. 1996). Specific delay-tuned neurons and neurons encoding azimuth and elevation of objects have been found, which are thought to be for directing head aim (Valentine & Moss, 1997).

TOOTHED WHALES: NEURAL STRUCTURES AFFECTED BY ECHOLOCATION

Due to ethical and practical considerations, considerably less research has been done on neural structures in odontocetes compared to echolocating bats. Although there is a paucity of information on exact structure of brain regions and types of neurons, hypertrophy has been found in certain brain structures of the auditory pathway and in sensorimotor pathways. Also, sensitivity to echo-like sounds has been found (Bullock et al. 1968; Supin et al. 2004). I will now discuss affected brain regions of the auditory pathway and sensorimotor pathways in toothed whales.

Auditory System

Cochlear Nucleus

The CN in odontocetes is highly enlarged, (de Graaf, 1967; Schwerdtfeger, 1984; Schulmeyer et al. 2000; Oelschlager et al. 2008; 2010), as is the auditory nerve, the largest of all cranial nerves in odontocetes (Schwerdtfeger et al. 1984; Marino, 2007; Oelschlager et al. 2010; Montie et al. 2007), presumably to transfer large amounts of auditory information to the nuclei of the auditory pathway. The auditory nerve is also much larger than in humans (Oelschlager et al. 2010). Interspecific differences in CN size are also evident, with river dolphins having the largest CN (Schwerdtfeger et al. 1984).

The VCN is the nucleus accounting for the enlargement of the CN, as the DCN seems to be rudimentary in odontocetes or even lacking in some species (Schulmeyer et al. 2000; Oelschlager et al. 2008; 2010). The VCN is approximately 150 times as large and contains fifteen times more neurons in the common dolphin (*Delphinus delphis*), with a brain mass of approximately 800 g, as the VCN in human beings, with a brain mass of about 1400 g (Oelschlager et al. 2008).

Superior Olivary Complex

The SOC is enlarged in odontocetes, and seems to be even more enlarged in river dolphins (Schwerdtfeger et al. 1984). Just like the VCN, it is approximately 150 times as large and contains approximately fifteen times more neurons in the common dolphin (*D. delphis*) than in the human (Oelschlager et al. 2008). The SOC of the riverine La Plata dolphin (*Pontoporia blainvillei*), with a brain of approximately 220 grams, is approximately 50 times as large as in humans (Oelschlager et al. 2008). The MNTB is hypertrophied as well, and bulges out of its normal position (de Graaf, 1967; Schwerdtfeger et al. 1984; Schulmeyer et al. 2000; Oelschlager et al. 2010).

Not all odontocete species show two distinct superior olivary nuclei, the LSO and MSO. The LSO is highly hypertrophied and extremely enlarged in all echolocating odontocetes (Schulmeyer et al. 2000), but the MSO only appears to exist in larger species of cetaceans, i.e. large toothed whales, such as the North Atlantic bottlenose whale (*Hyperoodon ampullatus*), the killer whale (*Orcinus orca*) and several species of baleen whale. This MSO is larger in these toothed whales than in the baleen whales (de Graaf, 1967), indicating specialized use for the MSO in echolocation.

Nuclei of Lateral Lemniscus

The NLL is, like all other auditory nuclei in the brainstem, highly enlarged in toothed whales (de Graaf, 1967; Schwerdtfeger et al. 1984; Marino et al. 2001; Schulmeyer et al. 2000; Oelschlager et al. 2008; 2010). A similar region as the VNLLc in bats has been found in dolphins, although its function is little understood (Glezer et al. 1998). In river dolphins, it seems even more developed (Schwerdtfeger et al. 1984).

Inferior Colliculus

The IC in the midbrain is very large in toothed whales in general, with a size several times larger than its neighbouring nucleus, the SC (de Graaf 1967; Schwerdtfeger et al. 1984; Schulmeyer et al. 2000; Marino et al. 2001), and has high energy needs for processing and sensory integration of auditory information (Houser et al. 2010). In river dolphins, the IC seems to be even more hypertrophied (Schwerdtfeger et al. 1984).

The IC does not seem to respond to low frequency sounds (<5 kHz) or longer duration sounds (>5 ms), indicating it is only used for processing of echolocation signals (Houser et al. 2010). The IC seems to possess high neuronal organization, with domain and interdomains evident in cytoarchitecture (Glezer et al. 1998). In addition to horizontal lamination patterns in terrestrial mammals, a vertical columnar pattern has been found in the bottle nose dolphin (*T. truncatus*), which likely indicates a highly specialized adaptation to process auditory information, i.e. coding of frequency bands of echolocation signals (Glezer et al. 1998). See figure 3.6 for the relative size of the IC in the bottlenose dolphin (*T. truncatus*) compared to the IC of a non-echolocating animal, the long-tailed macaque.

Auditory Thalamus

The auditory thalamus responds to echolocation signals (Bullock et al. 1968) and is very hypertrophied in the several investigated odontocete species, and is especially enlarged in river dolphins (Schwerdtfeger et al. 1984; Marino, 2007; Oelschlager et al. 2008; 2010). This enlargement is due to the MGN, which shows laminar arrangements of neurons (Glezer et al. 1998), indicating a specialized function in processing of temporal and spectral parameters of auditory signals. See figure 3.6 for relative size of the MGN compared to the lateral geniculate body, which belongs to the visual system, in dolphins and to the size of the IC in a non-echolocating mammal, the long-tailed macaque.

Auditory Cortex

As all auditory regions in the brain, the auditory cortex is enlarged as well (Marino, 2007; Oelschlager, 2008; Oelschlager et al. 2008). It is actually larger than all the other sensory cortical fields combined (Oelschlager et al. 2008) and has high energy needs for processing of auditory information (Houser et al. 2010). It does have a different position in the neocortex than in other mammalian species, possibly to do with the specialization for echolocation of this brain region (Glezer et al. 1998; Fung et al. 2005; Hof et al. 2005). It is very similar in cytoarchitecture to the visual cortex. See figure 3.6 for a comparison of the size and position of the AC in the bottlenose dolphin and the non-echolocating long-tailed macaque.

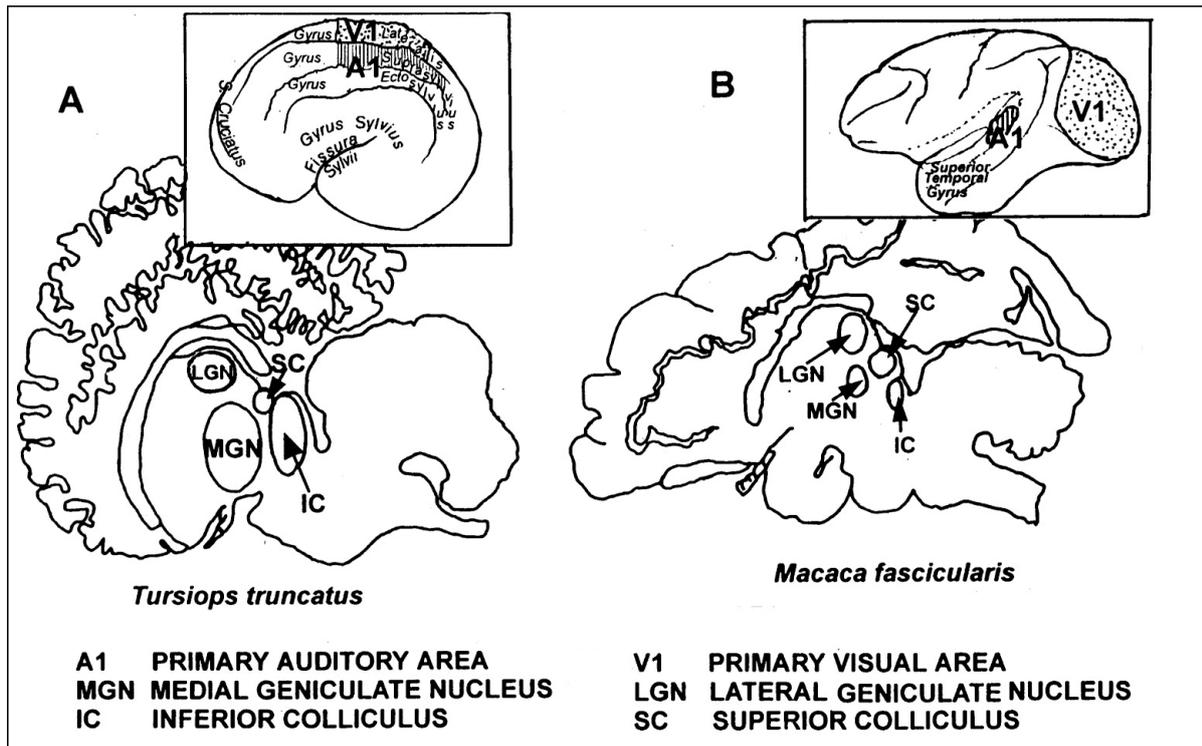


Figure 3.6 Cortical and subcortical brain structures in the visual and auditory systems of the brains of bottlenose dolphin (*T. truncatus*) and the long-tailed macaque (*Macaca fascicularis*). Figure A shows the brain of *T. truncatus*, showing the LGN, SC and V1 of the visual system and the MGN, IC and A1 of the auditory system. The same has been shown in figure B for *M. fascicularis*. Note the differences in size of the MGN, LGN, IC and AC and the different position of A1 and V1 in both species. Modified from Glezer et al. 1998

Sensorimotor System

Cerebellum and Associated Nuclei

Marino et al. (2000) found relative cerebellum volume of two dolphin species, the common and the bottlenose dolphin to be significantly higher, on average fifteen percent, than in several primate species. This indicates the cerebellum is highly developed and enlarged in odontocetes.

Several other nuclei located in the brainstem relay information to the cerebellum and have been associated with audiomotor navigation in toothed whales. Namely the elliptic nucleus, several pontine nuclei and the inferior olivary complex have been deemed important in linking auditory information from the auditory pathway to the motor pathways (Oelschlager, 2008; Oelschlager et al. 2010).

Facial Nucleus and Nerve

The facial nerve and nucleus are hypertrophied, and found to be relatively larger in toothed whales than in non-echolocating baleen whales (de Graaf, 1967) and other mammals (Oelschlager, 2008). The facial nerve and associated nucleus are thought to control sound production for echolocation and communication by the sound-generating complex in the odontocetes' head (Huggenberger et al. 2009; Oelschlager et al. 2010).

Trigeminal Nerves

The trigeminal nerve appears to be well developed in odontocetes and has relatively high axon numbers (Schwerdtfeger et al. 1984; Oelschlager et al. 2010). It is thought to be associated with prey seeking through vibrissae and for control of the sound generating complex in the odontocetes' head (Schwerdtfeger et al. 1984), together with the facial nerve and associated nucleus (Oelschlager et al. 2010).

DISCUSSION

Neural structures follow function, and functions are dictated by the ecology of a species. Neural adaptations for echolocation is an interesting example, giving the fact that it is a highly specialized use of a sensory modality, and occurs in animals with vastly different ecologies, such as echolocating bats and toothed whales. These differences in ecology must have caused differences in echolocating abilities and must thus be evident in the brain regions involved in echolocation.

This thesis provides an overview of the general ecology of both echolocating bats and toothed whales and the brain regions in the auditory and sensorimotor pathways that are involved in echolocation. General similarities and differences in the auditory and sensorimotor systems between echolocating bats, toothed whales and the 'standard' mammalian brain in relation to their ecology will be discussed, as well as evolutionary aspects in regard to echolocation in the two mammalian groups.

Similarities and Differences in the Auditory System of Bats and Toothed Whales

In general, almost all nuclei of the auditory system are highly hypertrophied in both bats and toothed whales. Nuclei in the brainstem, midbrain and auditory thalamus and the auditory cortex are highly enlarged, which is thought to enable the complex processing of echolocation pulse and echo parameters (Oelschlager, 2008).

In river dolphins, specific nuclei are even more hypertrophied compared to relatives living in less turbid and cluttered environments. The CN, SOC, NLL, IC and AT are especially enlarged in these species and indicate their importance in processing of echoes (Schwerdtfeger et al. 1984). In echolocating bats, a similar trend of relatively large sizes can be observed according to size of specific nuclei, with bats using CF-components, an adaptation to foraging in highly cluttered environments, such as an extremely hypertrophied MSO (Grothe & Park, 2000)

Ecology influences call design, and this is evident in the tuning properties of neurons in bats, which are in accordance to important temporal and spectral parameters of the species audiogram (Ma & Suga, 2009). Specific tonotopies are evident from the CN all the way up to the AC. In species using CF-components in the pulses, these frequencies are highly overrepresented and form acoustic foveas. These CF representations are a special adaptation to foraging in dense foliage, and are highly important for classifying prey through SFM and SAM and assessing relative speed through Doppler-shift (Schnitzler & Kalko, 2001). FM-components of echolocation pulses are also overrepresented in the auditory system of bats that use them, which are highly important for precise localization of prey items. In species using passive listening to detect prey, these lower frequencies are also represented (see fig. 3.5) (Fuzessery & Hall, 1999).

Delay-tuned neurons are also found in the auditory system, and distinctions according to ecology can be made. Species-specific sensing distances of bats can actually be obtained through examining the dispersal of response latencies, which responds to target distance, in collicular neurons (Goto, 2010). In the IC, different amounts of PLS-neurons have been found between CF-FM bats and FM bats (Ma & Suga, 2008; Klug et al. 2000; Galazyuk & Feng, 2001). This is possibly due to the fact that CF-FM bats need intensity-independent neurons to assess echo delay, as they assess the delay between the first harmonic of the pulse with the first harmonic of the echo, which is less intense due to attenuation. FM bats do not need this intensity-independent detection, as they compare the first harmonic of the pulse with a higher harmonic of the returning echo, which is emitted at higher intensity and thus does not return much weaker than the first harmonic pulse (Yan & Suga, 1996; Feng, 2010). However, the results of different amounts of PLS-neurons could have also resulted due to diverging methods of analysis, as Feng (2010) points out.

Other adaptations according to call design are evident with tuning to specific intensities and pulse durations of calls. Also highly modular regions are found in the upstream nuclei, all according to specific pure tones, SFM/SAM's, frequency sweeps or Doppler-shifts. However, although neurons are tuned to specific pulse parameters, they are not only existent in echolocating bats. Similar neurons were already present in the standard mammalian brain. It does not seem that distinct new types of neurons for echolocation parameters needed to evolve. Only different tuning properties, e.g. to higher frequencies or to specific FM sweeps, are essential for the processing of echolocation signals (Covey, 2005).

Not much is known on the neuronal properties in toothed whales, but it would be expected it is similarly tuned to important echolocation parameters, as it has evolved out of the standard mammalian bauplan. Almost no research has been done on the neuronal structure of nuclei of the auditory system in toothed whales, but several studies have indicated that the toothed whale's brain does show sensitivity to specific frequencies (such as frequency sweeps), intensities (high echolocation intensities) and durations (very short durations associated with echolocation pulses and echoes) (Bullock et al. 1968; Supin et al. 2004; Houser et al. 2010). Although the brain in echolocating bats and toothed whales seems to be similar in its basic anatomy, there are some remarkable adaptations. The SOC comprises of interesting specializations, or complete lack there of, in both toothed whales and bats. The LSO and MNTB are very similar to non-echolocating mammals, although highly enlarged, and function in processing IID's and thus determining azimuth of objects (Grothe & Park, 2000). The MSO however, is especially interesting. Being non-existent or hypotrophied in most small, high frequency mammals, due to the lack of detectable ITD's, it is quite surprising to see that it is highly enlarged in echolocating bats. First of all, there may be mechanisms for such small animals using high frequency sounds to still make use of ITD's. By using response latencies and IID's, with shorter latencies for stronger intensities, differences in arrival time at neurons in the MSO can be enlarged neurally, thus creating usable ITD's. It has however been shown that in CF-FM bats, the MSO is extremely enlarged and contains mostly monaural neurons. It seems to be adapted to play a different functional role than in the normal mammalian MSO. First of all, it may function in pattern recognition, setting up selectivity for specific modulations for the IC (Grothe et al. 1997; Casseday et al. 1997). The extreme enlargement of the MSO in CF-FM bats does support this, as the CF-component of calls is used for prey recognition, i.e. processing of SFM and SAM (Grothe et al. 2001).

A possible second or alternative function for the MSO is to process communication calls (Grothe et al. 2001), especially in reverberant rooms such as caves (Pollak et al. 2002). Bats often inhabit caves in large groups and use communication signals. These signals however reflect off the walls and reverberate back to the bat, creating a cacophony of sounds. This calls for the need to be able to separate acoustic information from second sound sources or sound reflections and merging different sounds from the same sound source (Grothe & Park, 2000). This can be accomplished by creating a spatio-temporal map of sounds in the MSO (Grothe & Park, 2000).

Another specialization is the VNLLc in echolocating bats (Covey & Casseday, 1986), and it may also exist in toothed whales, as vertical columniation has been found in the VNLL and IC in this group (Glezer et al. 1998). Its function in bats is believed to lay in the extraction of precise time markers across each frequency band, and thus serves in precise localization of targets (Covey & Casseday, 1986; Haplea et al. 1994). Although a similar structure as the VNLLc in bats has been found in toothed whales as well, its function is not well understood. It is very likely it has a similar function. Having exact time markers in toothed whales is likely to be more difficult in toothed whales due to the medium they live in and the faster pulse repetition rates they exhibit, calling for high temporal resolution. This could be the reason there is additional vertical columniation in the IC in toothed whales, although its exact function is little understood.

The AC has shifted to a different position in toothed whales compared to the standard mammalian brain (Glezer et al. 1998; Fung et al. 2005; Hof et al. 2005). This could possibly

be due to specialization according to echolocation, although not much is known on why its location has changed in toothed whales.

The DCN in bats is not hypertrophied and does not display distinct lamination (Covey & Casseday, 1995). In toothed whales, the DCN is highly reduced or even lacking, and does not seem to possess any function. Schulmeyer et al. (2000) proposed a theory that the DCN might be active in processing auditory artifact caused by movements of the pinna relative to the head or a sound source. In several mammalian species, there seems to be a correlation between the amount of lamination and the presence/mobility of the pinna (Schulmeyer et al. 2000). However, a bigger DCN in bats would be suspected as well, as they need to actively move their pinna to optimally receive echoes. The mammals noted to have highly mobile pinna and a well-laminated DCN are relatively large compared to bats and use low frequency sounds (e.g. cats). Perhaps these auditory artifacts are less pronounced in bats due to their smaller size and smaller movements of the pinna, or due to the use of high frequency sounds, versus low frequency sounds.

Similarities and Differences in the Sensorimotor System of Bats and Toothed Whales

Bats and toothed whales have to incorporate their perception of the environment through echolocation to their motor systems. Both mammalian groups are able to move quickly through 3D environments. However, their morphologies are very different, causing remarkable divergences in what brain regions are involved.

The cerebellum is enlarged in both bats and toothed whales, although it does seem more specialized in the latter (Marino et al. 2000; Oelschlager, 2008). Also, nuclei connecting the cerebellum to the neocortex are hypertrophied in both groups, which is likely due to the coupling of the very large auditory system to the sensorimotor system (Oelschlager et al. 2008). This is evident in the proliferation of cerebellar areas involved in acoustic processing (Marino et al. 2000). The cerebellum is involved in the coordination and thus very important for moving quickly through 3D environments (Schwerdtfeger et al. 1984; Marino et al. 2000). It has actually been found to be less hypertrophied in river dolphins, most likely due to the fact that they move slower than their marine relatives (Schwerdtfeger et al. 1984).

In toothed whales however, the cerebellum is likely not only involved in locomotion, but also in the fast processing of acoustic information to be able to localize objects, explaining its highly hypertrophied state (Oelschlager, 2008). Fast processing is especially needed in toothed whales due to the fast traveling speed of sound in water, calling for rapid dynamic processing of echoes (Oelschlager et al. 2008; Marino et al. 2000).

The SC seems to be especially important in echolocating bats, but not whales. In bats, the SC is a specialization for the pursuit of insects, coordinating the movements of the head and pinna to optimally emit and receive echolocation pulses and echoes for catching prey. These movements can be seen as the auditory equivalent of eye movements, i.e. saccades (Valentine et al. 2002). Although there is no large difference in SC size between mega- and microchiropterans (Hu et al. 2006), there is far less auditory input to the SC in megachiropterans. Megachiropterans are highly dependent on their vision, and the SC can still be involved in orienting head movements using vision, explaining its relatively large size. Toothed whales do not show hypertrophy of the SC and this is likely due to the fact that they lack external pinna and have evolved long spindled bodies, which restrict head movements. Instead, they need to rely more on the formation of acoustic beams through their sound generating epicranial complex, which concerns other motor areas (Schwerdtfeger et al. 1984; Schulmeyer et al. 2000).

The epicranial complex, comprising of the nasal complex and the melon, is controlled by the facial nucleus and associated nerve and the trigeminal nerve. The facial nucleus and nerve are well developed for the control of the nasal complex, i.e. echolocation pulse production via the phonic lips. The trigeminal nerve is associated with the control of the lemon (Schwerdtfeger et al. 1984), i.e. to aim echolocation pulses, explaining why it is so well developed.

Toothed whales have different sensitivities for sound on their jaw and head, and they can use these different sensitivities to sense the direction of a sound source. Possibly, the trigeminal nerve is used in assessing the intensities, and thus direction, of sound vibrations, as the trigeminal nerve is associated with sensitization of the face (Purves et al. 2004).

Bats do not use their nasal complex to generate sounds, thus explaining why the facial nucleus, facial nerve and trigeminal nerve are not as well developed as in toothed whales. In bats, echolocation pulses are emitted via the larynx, which is controlled by different neural structures (Rubsamen & Betz, 1986).

Evolutionary Aspects

Although echolocating bats and dolphins have been separated for at least 55 million years (Marino et al. 2001), convergent evolution appears to have happened in regard to echolocation. A specific gene involved in hearing of high frequency sounds has been found in both mammalian groups (Li et al. 2010). I will now discuss several interesting aspects of the evolution of echolocation.

It has been speculated that the relatively large brain of toothed whales, especially oceanic delphinids (Schwerdtfeger et al. 1984; Oelschläger et al. 2010), has evolved due to their echolocation abilities. Although the auditory pathway is highly enlarged, their large brain is not likely to have formed solely due to echolocation. Other echolocating species, such as bats, do not show these high encephalization indices, showing that echolocation does not necessarily call for a big brain. Neither do all species with large brains echolocate (Marino, 2007). Echolocation thus does not seem the direct cause for brain enlargement in toothed whales and is more likely due to their high cognitive capabilities and complex social behaviours, such as coalition formation, cooperation, cultural transmission and tool use (Hof et al. 2005). This is mostly evident through the large neocortical region (Marino, 2007).

One very interesting evolutionary aspect is the energy expense involved with echolocation. Echolocation is potentially costly, as the complex processing of sound signals requires energy, as does the generation of high intensity sounds. Emitting echolocation pulses in bats at rest has been shown to cost at least ten times more energy as in resting state (Altringham, 1996). However, bats have evolved a very cost-effective way of echolocation. This may have been the cause that it has evolved to be the primary sensory system in bats. Bats are able to very economically use the energy of wing movements to keep echolocation costs to a minimum, not actually differing in energy expenditure with non-echolocating bats or birds in flight (Speakman & Racey, 1991).

However, if echolocation is such an economical activity for toothed whales is questionable. Little is known on energy expenditure regarding echolocation in toothed whales. They do not seem to have a similar way of minimizing energy expenditure by echolocation as bats do. Combined with the energy expense of acoustic processing, this would make echolocation a highly costly activity. They also have an added disadvantage, as they have to cope with high physiological demands when diving, such as oxygen deprivation and high diving pressures (Kooyman, 2002; Houser et al. 2010). There may be lower cost of sound generation involved with the epicranial complex than the larynx, although little research has been done on this subject. It has been shown that deep divers do have lower number of neurons in their brain to cope with oxygen-deprivation (Poth et al. 2005) and control of vascular systems to provide oxygen to specific auditory processing centers are also expected (Houser et al. 2010). Although little is known on the subject, it would be interesting to know if and how energy expenditure has influenced the evolution of echolocation in toothed whales.

Conclusion

Differences in neural structures are evident between different bat species, between different dolphin species and between the two mammalian groups, and can be related to ecological and morphological differences. The auditory system is highly enlarged in both groups of mammals. Tuning to species-specific audiogram parameters is evident in bats in all nuclei,

such as frequency, intensity or pulse duration. In more specialized species, such as CF-FM bats or river dolphins, more extreme hypertrophy of certain brain structures is found. Several remarkable adaptations have been found in both bats and toothed whales. The MSO in bats is highly specialized according to call design, and likely functions in pattern recognition for prey detection and classification in CF bats and/or enabling the filtering of reverberances. In the smaller toothed whale species, the MSO has disappeared as no ITD's can be processed with high frequency sounds, small-sized head and high sound velocity in water, while in larger, lower frequency species it is still evident. The VNLLc in bats is another specialization and has most likely evolved for precise target localization. A similar structure exists in the toothed whales' NLL and IC, although its function is not yet understood. Hypotrophy of the DCN is evident in toothed whales, and may be due to their lack of external pinna. Several nuclei involved in sensorimotor processing are hypertrophied, and differences between bats and toothed whales seem to arise mostly due to the sound carrying properties of water and morphological differences in sound generation and perception.

The convergent evolution of echolocation in bats and toothed whales is evident in their genetics. Although echolocation is very energy efficient in bats, and possibly the reason it has evolved to the extent it has, this is not evident in toothed whales, which have to cope with the physiological demands of diving. Also, in toothed whales, echolocation is likely to not have caused the extreme encephalization in these species.

Call design is evident through ecology, morphology and the amount of clutter a species has to navigate through. This has obviously influenced the size and tuning of neural structures involved in auditory processing. Similarly, adaptations in sensorimotor pathways have been made to cope with sound generation, sound reception and ability to move through a 3D environment. The ability to echolocate is clearly evident in the associated neural structures in echolocating bats and toothed whales and can be related to their respective ecologies.

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References

- Altringham, J.D. (1996) Bats: biology and behaviour. Oxford Univ. Press, Oxford.
- Au, W.W. (2002) Echolocation. In Perrin W.F., Wursig, B., Thewissen, J.G. (eds), Encyclopedia of Marine Mammals, Ac. Press, San Diego, pp. 358–367
- Au, W.W. (2004) Introduction: a comparison of the sonar capabilities of bats and dolphins. In Thomas, J.A., Moss, C.F., Vater, M. (eds.) Echolocation in Bats and Dolphins, Uni. of Chicago Press, Chicago, pp. xiii-xxvii
- Au, W. W., Moore, P.W. & Pawloski, D.A. (1988) Detection of complex echoes in noise by an echolocating dolphin. J. Acoust. Soc. Am., **83**, 662-668.
- Au, W.W., Simmons, J.A. (2007) Echolocation in dolphins and bats. Phys. Tod., **60**, 40-45
- Au, W. W., Branstetter, B.K., Benoit-Bird, K.J. & Kastelein, R.A. (2009) Acoustic basis for fish prey discrimination by echolocating dolphins and porpoises. J. Acoust. Soc. Am., **126**, 460-467.
- Bjorge, A., Tolley, K.A. (2002) Harbour Porpoise. In Perrin W.F., Wursig, B., Thewissen, J.G. (eds), Encyclopedia of Marine Mammals, Ac. Press, San Diego, pp. 549–551.
- Bullock, T.H., Grinnell, A.D., Ikezono, E., Kameda, K., Katsuki, Y., Nomoto, M., Sato, O., Suga, N., Yanagisawa, K. (1968) Electrophysiological studies of central auditory mechanisms in cetaceans. Z. vergleich. Phys., **59**, 117-156
- Casseday, J. H., Ehrlich, D. & Covey, E. (1994) Neural tuning for sound duration: Role of inhibitory mechanisms in the inferior colliculus. Science, **264**, 847-850.
- Casseday, J. H., Covey, E. & Grothe, B. (1997) Neural selectivity and tuning for sinusoidal frequency modulations in the inferior colliculus of the big brown bat, *Eptesicus fuscus*. J. Neurophysiol., **77**, 1595-1605.
- Casseday, J. H., Ehrlich, D. & Covey, E. (2000) Neural measurement of sound duration: Control by excitatory-inhibitory interactions in the inferior colliculus. J. Neurophysiol., **84**, 1475-1487.
- Covey, E. (2005) Neurobiological specializations in echolocating bats. Anat. Rec. A. Discov. Mol. Cell. Evol. Biol., **287**, 1103-1116.
- Covey, E. & Casseday, J.H. (1991) The monaural nuclei of the lateral lemniscus in an echolocating bat: Parallel pathways for analyzing temporal features of sound. J. Neurosci., **11**, 3456-3470.
- Covey, E., Casseday, J.H. (1995) The lower brainstem auditory pathways. In Popper, A.N., Fay, R.R. (eds) Hearing by Bats, Springer-Verlag, New York, pp. 191–295.
- Covey, E., Kauer, J.A. & Casseday, J.H. (1996) Whole-cell patch-clamp recording reveals subthreshold sound-evoked postsynaptic currents in the inferior colliculus of awake bats. J. Neurosci., **16**, 3009-3018.
- Covey, E. & Casseday, J.H. (1999) Timing in the auditory system of the bat. Annu. Rev. Physiol., **61**, 457-476.
- Covey, E. & Casseday, J.H. (1986) Connectional basis for frequency representation in the nuclei of the lateral lemniscus of the bat *Eptesicus fuscus*. J. Neurosci., **6**, 2926-2940.
- Cranford, T. W., Amundin, M. & Norris, K.S. (1996) Functional morphology and homology in the odontocete nasal complex: Implications for sound generation. J. Morphol., **228**, 223-285
- De Graaf, A.S. (1967) Anatomical aspects of the cetacean brain stem. Van Gorcum and Prakke, Assen

- Denzinger, A., Kalko, E.K., Jones, G. (2004) Introduction: ecological and evolutionary aspects of echolocation in bats. In Thomas, J.A., Moss, C.F., Vater, M. (eds.) *Echolocation in Bats and Dolphins*, Uni. of Chicago Press, Chicago, pp. 311-326
- Faure, P. A., Fremouw, T., Casseday, J.H. & Covey, E. (2003) Temporal masking reveals properties of sound-evoked inhibition in duration-tuned neurons of the inferior colliculus. *J. Neurosci.*, **23**, 3052-3065.
- Feng, A. S. (2010) Neural mechanisms of target ranging in FM bats: Physiological evidence from bats and frogs. *J. Comp. Physiol. A. Neuroethol Sens. Neural Behav. Physiol.*, *in press*
- Fenton, M.B. (1984) Implications for ecology and evolution of bats: *Q. Rev. Biol.*, **59**, 33-53
- Firzlaff, U., Schuchmann, M., Grunwald, J.E., Schuller, G. & Wiegrebe, L. (2007) Object-oriented echo perception and cortical representation in echolocating bats. *PLoS Biol.*, **5**, 1174-1183.
- Fremouw, T., Faure, P.A., Casseday, J.H. & Covey, E. (2005) Duration selectivity of neurons in the inferior colliculus of the big brown bat: Tolerance to changes in sound level. *J. Neurophysiol.*, **94**, 1869-1878.
- Fung, C., Schleicher, A., Kowalski, T. & Oelschlager, H.H. (2005) Mapping auditory cortex in the la plata dolphin (*Pontoporia blainvillei*). *Brain Res. Bull.*, **66**, 353-356.
- Fuzessery, Z. M. & Hall, J.C. (1999) Sound duration selectivity in the pallid bat inferior colliculus. *Hear. Res.*, **137**, 137-154.
- Fuzessery, Z.M., Richardson, M.D., Coburn, M.S. (2006) Neural mechanisms underlying selectivity for rate and direction of frequency-modulated sweeps in the inferior colliculus of the pallid bat. *J. Neurophysiol.*, **96**, 1320-1336
- Galazyuk, A. V. & Feng, A.S. (2001) Oscillation may play a role in time domain central auditory processing. *J. Neurosci.*, **21**, RC147.
- Gaskin, D.E., (1982) *The ecology of whales and dolphins*. Heinemann, London.
- Glezer, I. I., Hof, P.R. & Morgane, P.J. (1998) Comparative analysis of calcium-binding protein-immunoreactive neuronal populations in the auditory and visual systems of the bottlenose dolphin (*Tursiops truncatus*) and the macaque monkey (*Macaca fascicularis*). *J. Chem. Neuroanat.*, **15**, 203-237.
- Goto, K., Hiryu, S. & Riquimaroux, H. (2010) Frequency tuning and latency organization of responses in the inferior colliculus of japanese house bat, *Pipistrellus abramus*. *J. Acoust. Soc. Am.*, **128**, 1452-1459.
- Grothe, B. (2000) The evolution of temporal processing in the medial superior olive, an auditory brainstem structure. *Prog. Neurobiol.*, **61**, 581-610.
- Grothe, B., Vater, M., Casseday, J.H. & Covey, E. (1992) Monaural interaction of excitation and inhibition in the medial superior olive of the mustached bat: An adaptation for biosonar. *Proc. Natl. Acad. Sci. U. S. A.*, **89**, 5108-5112.
- Grothe, B., Park, T.J. & Schuller, G. (1997) Medial superior olive in the free-tailed bat: Response to pure tones and amplitude-modulated tones. *J. Neurophysiol.*, **77**, 1553-1565.
- Grothe, B. & Park, T.J. (2000) Structure and function of the bat superior olivary complex. *Microsc. Res. Tech.*, **51**, 382-402.
- Grothe, B., Covey, E. & Casseday, J.H. (2001) Medial superior olive of the big brown bat: Neuronal responses to pure tones, amplitude modulations, and pulse trains. *J. Neurophysiol.*, **86**, 2219-2230.
- Haplea, S., Covey, E. & Casseday, J.H. (1994) Frequency tuning and response latencies at three levels in the brainstem of the echolocating bat, *Eptesicus fuscus*. *J. Comp. Physiol. A.*, **174**, 671-683.

- Herzing, D.L., dos Santos, M.E. (2004) Functional aspects of echolocation in dolphins. In Thomas, J.A., Moss, C.F., Vater, M. (eds.) *Echolocation in Bats and Dolphins*, Uni. of Chicago Press, Chicago, pp. 386-392
- Hof, P. R., Chanis, R. & Marino, L. (2005) Cortical complexity in cetacean brains. *Anat. Rec. A. Discov. Mol. Cell. Evol. Biol.*, **287**, 1142-1152.
- Holland, R. A., Waters, D.A. & Rayner, J.M. (2004) Echolocation signal structure in the megachiropteran bat *Rousettus aegyptiacus* geoffroy 1810. *J. Exp. Biol.*, **207**, 4361-4369.
- Houser, D. S., Moore, P.W., Johnson, S., Lutmerding, B., Branstetter, B., Ridgway, S.H., Trickey, J., Finneran, J.J., Jensen, E. & Hoh, C. (2010) Relationship of blood flow and metabolism to acoustic processing centers of the dolphin brain. *J. Acoust. Soc. Am.*, **128**, 1460-1466.
- Hu, K., Li, Y., Gu, X., Lei, H. & Zhang, S. (2006) Brain structures of echolocating and nonecholocating bats, derived in vivo from magnetic resonance images. *Neuroreport*, **17**, 1743-1746.
- Huggenberger, S., Rauschmann, M.A., Vogl, T.J. & Oelschlager, H.H. (2009) Functional morphology of the nasal complex in the harbor porpoise (*Phocoena phocoena* L.). *Anat. Rec. (Hoboken)*, **292**, 902-920.
- Ibsen, S. D., Au, W.W., Nachtigall, P.E. & Breese, M. (2009) Functional bandwidth of an echolocating atlantic bottlenose dolphin (*Tursiops truncatus*). *J. Acoust. Soc. Am.*, **125**, 1214-1221.
- Jones, G. & Teeling, E.C. (2006) The evolution of echolocation in bats. *Trends Ecol. Evol.*, **21**, 149-156.
- Klug, A., Khan, A., Burger, R.M., Bauer, E.E., Hurley, L.M., Yang, L., Grothe, B., Halvorsen, M.B., Park, T.J. (2000) Latency as a function of intensity in auditory neurons: influences of central processing. *Hear. Res.*, **148**, 107-123
- Kooyman, G.L. (2002) Diving physiology. In Perrin W.F., Wursig, B., Thewissen, J.G. (eds), *Encyclopedia of Marine Mammals*, Ac. Press, San Diego, pp. 339–344.
- Kossl, M. (1994) Evidence for a mechanical filter in the cochlea of the 'constant frequency' bats, *Rhinolophus rouxi* and *Pteronotus parnellii*. *Hear. Res.*, **72**, 73-80.
- Li, Y., Liu, Z., Shi, P., Zhang, J. (2010) *Cur. Biol.*, **20**, 55-56
- Luo, F., Metzner, W., Wu, F., Zhang, S. & Chen, Q. (2008) Duration-sensitive neurons in the inferior colliculus of horseshoe bats: Adaptations for using CF-FM echolocation pulses. *J. Neurophysiol.*, **99**, 284-296.
- Ma, X. & Suga, N. (2008) Corticofugal modulation of the paradoxical latency shifts of inferior collicular neurons. *J. Neurophysiol.*, **100**, 1127-1134.
- Macias, S., Mora, E.C., Kossl, M., Abel, C. & Foeller, E. (2009) The auditory cortex of the bat *Molossus molossus*: Disproportionate search call frequency representation. *Hear. Res.*, **250**, 19-26.
- Marino, L. (2007) Cetacean brains: How aquatic are they? *Anat. Rec. (Hoboken)*, **290**, 694-700.
- Marino, L., Rilling, J.K., Lin, S.K. & Ridgway, S.H. (2000) Relative volume of the cerebellum in dolphins and comparison with anthropoid primates. *Brain Behav. Evol.*, **56**, 204-211.
- Marino, L., Murphy, T.L., Gozal, L. & Johnson, J.I. (2001) Magnetic resonance imaging and three-dimensional reconstructions of the brain of a fetal common dolphin, *Delphinus delphis*. *Anat. Embryol. (Berl)*, **203**, 393-402.
- Marsh, R. A., Nataraj, K., Gans, D., Portfors, C.V. & Wenstrup, J.J. (2006) Auditory responses in the cochlear nucleus of awake mustached bats: Precursors to spectral integration in the auditory midbrain. *J. Neurophysiol.*, **95**, 88-105.
- Matsuo, I., Imaizumi, T., Akamatsu, T., Furusawa, M. & Nishimori, Y. (2009) Analysis of the temporal structure of fish echoes using the dolphin broadband sonar signal. *J. Acoust. Soc. Am.*, **126**, 444-450.

- Mittmann, D. H. & Wenstrup, J.J. (1995) Combination-sensitive neurons in the inferior colliculus. *Hear. Res.*, **90**, 185-191.
- Montie, E. W., Schneider, G.E., Ketten, D.R., Marino, L., Touhey, K.E. & Hahn, M.E. (2007) Neuroanatomy of the subadult and fetal brain of the atlantic white-sided dolphin (*Lagenorhynchus acutus*) from in situ magnetic resonance images. *Anat. Rec. (Hoboken)*, **290**, 1459-1479.
- Mooney, T.A., Whitlow, W.W., Nachtigall, P.E., Trippel, E.A. (2007) Acoustic and stiffness properties of gillnets as they relate to small cetacean bycatch. *ICES J. Mar. Sc.*, **64**, 1324-1332
- Neuweiler, G. (2003) Evolutionary aspects of bat echolocation. *J. Comp. Physiol.*, **189**, 245-256
- Oelschläger, H. H. (2008) The dolphin brain--a challenge for synthetic neurobiology. *Brain Res. Bull.*, **75**, 450-459.
- Oelschläger, H. H., Haas-Rioth, M., Fung, C., Ridgway, S.H. & Knauth, M. (2008) Morphology and evolutionary biology of the dolphin (*Delphinus* sp.) brain--MR imaging and conventional histology. *Brain Behav. Evol.*, **71**, 68-86.
- Oelschläger, H. H., Ridgway, S.H. & Knauth, M. (2010) Cetacean brain evolution: Dwarf sperm whale (*Kogia sima*) and common dolphin (*Delphinus delphis*) - an investigation with high-resolution 3D MRI. *Brain Behav. Evol.*, **75**, 33-62.
- Pollak, G.D., Park, T.J. (1995) 'The inferior Colliculus': In Popper, A.N., Fay, R.R. (eds) *Hearing by Bats*, Springer-Verlag, New York, pp. 296-367.
- Pollak, G. D., Burger, R.M., Park, T.J., Klug, A. & Bauer, E.E. (2002) Roles of inhibition for transforming binaural properties in the brainstem auditory system. *Hear. Res.*, **168**, 60-78.
- Portfors, C. V. & Wenstrup, J.J. (2001) Topographical distribution of delay-tuned responses in the mustached bat inferior colliculus. *Hear. Res.*, **151**, 95-105.
- Purves, D., Augustine, G.J., Fitzpatrick, D., Hall, W.C., LaMantia, A., McNamara, J.O., Williams, S.M. (2004) *Neuroscience*, third ed., Sinauer Associates, Sunderland, MA.
- Razak, K. A. & Fuzessery, Z.M. (2009) GABA shapes selectivity for the rate and direction of frequency-modulated sweeps in the auditory cortex. *J. Neurophysiol.*, **102**, 1366-1378.
- Rubsamen, R. & Betz, M. (1986) Control of echolocation pulses by neurons of the nucleus ambiguus in the rufous horseshoe bat, *Rhinolophus rouxi*. I. single unit recordings in the ventral motor nucleus of the laryngeal nerves in spontaneously vocalizing bats. *J. Comp. Physiol. A.*, **159**, 675-687.
- Sachs, M.B., Blackburn, C.C., (1991) Processing of complex sounds in the cochlear nucleus. In Altschuler, R.A. (ed) *Neurobiology of Hearing: the Central Auditory System*. Raven Press, New York.
- Sanderson, M. I. & Simmons, J.A. (2000) Neural responses to overlapping FM sounds in the inferior colliculus of echolocating bats. *J. Neurophysiol.*, **83**, 1840-1855.
- Schnitzler, H., Kalko, E.K. (2001) Echolocation in insect-eating bats. *Bioscience*, **51**, 557-569
- Schnitzler, H., Moss, C.F., Denzinger, A. (2003) From spatial orientation to food acquisition in echolocating bats. *Tr. Ecol. Evol.*, **18**, 385-394
- Schulmeyer, F.J., Adams, J.C., Oelschläger, H.H. (2000) Specialized sound reception in dolphins – a hint for the function of the dorsal cochlear nucleus in mammals. *Hist. Biol.*, **14**, 53-56
- Schwerdtfeger, W. K., Oelschläger, H.A. & Stephan, H. (1984) Quantitative neuroanatomy of the brain of the La Plata dolphin, *Pontoporia blainvillei*. *Anat. Embryol. (Berl)*, **170**, 11-19.

- Simmons, J. A., Lavender, W.A., Lavender, B.A., Doroshov, C.A., Kiefer, S.W., Livingston, R., Scallet, A.C. & Crowley, D.E. (1974) Target structure and echo spectral discrimination by echolocating bats. *Science*, **186**, 1130-1132.
- Simmons, J.A., Stein, R.A. (1980) Acoustic imaging in bat sonar: echolocation signals and the evolution of echolocation. *J. Comp. Physiol.*, **135**, 61-84
- Sinha, S. R. & Moss, C.F. (2007) Vocal premotor activity in the superior colliculus. *J. Neurosci.*, **27**, 98-110.
- Solntseva, G. N. & Rodionov, V.A. (2007) Structural and functional organization of sound generation and sound perception organs in dolphins. *Dokl. Biol. Sci.*, **417**, 476-479.
- Speakman, J. R. & Racey, P.A. (1991) No cost of echolocation for bats in flight. *Nature*, **350**, 421-423.
- Suga, N., O'Neill, W.E. & Manabe, T. (1978) Cortical neurons sensitive to combinations of information-bearing elements of biosonar signals in the mustached bat. *Science*, **200**, 778-781.
- Supin, A. Y., Nachtigall, P.E., Au, W.W. & Breese, M. (2004) The interaction of outgoing echolocation pulses and echoes in the false killer whale's auditory system: Evoked-potential study. *J. Acoust. Soc. Am.*, **115**, 3218-3225.
- Szymanski, M. D., Bain, D.E., Kiehl, K., Pennington, S., Wong, S. & Henry, K.R. (1999) Killer whale (*Orcinus orca*) hearing: Auditory brainstem response and behavioral audiograms. *J. Acoust. Soc. Am.*, **106**, 1134-1141.
- Thiele, A., Rubsamen, R. & Hoffmann, K.P. (1996) Anatomical and physiological investigation of auditory input to the superior colliculus of the echolocating megachiropteran bat *Rousettus aegyptiacus*. *Exp. Brain Res.*, **112**, 223-236.
- Ulanovsky, N. & Moss, C.F. (2008) What the bat's voice tells the bat's brain. *Proc. Natl. Acad. Sci. U. S. A.*, **105**, 8491-8498.
- Valentine, D. E. & Moss, C.F. (1997) Spatially selective auditory responses in the superior colliculus of the echolocating bat. *J. Neurosci.*, **17**, 1720-1733.
- Valentine, D. E., Sinha, S.R. & Moss, C.F. (2002) Orienting responses and vocalizations produced by microstimulation in the superior colliculus of the echolocating bat, *Eptesicus fuscus*. *J. Comp. Physiol. A. Neuroethol Sens. Neural Behav. Physiol.*, **188**, 89-108.
- Vater, M., Foeller, E., Mora, E.C., Coro, F., Russell, I.J. & Kossl, M. (2010) Postnatal maturation of primary auditory cortex in the mustached bat, *Pteronotus parnellii*. *J. Neurophysiol.*, **103**, 2339-2354.
- Vater, M. & Kossl, M. (2010) Comparative aspects of cochlear functional organization in mammals. *Hear. Res.*, *in press*
- Wenstrup, J. J., Mittmann, D.H. & Grose, C.D. (1999) Inputs to combination-sensitive neurons of the inferior colliculus. *J. Comp. Neurol.*, **409**, 509-528.
- Whitehead, H. (2002) Sperm whale. In Perrin W.F., Wursig, B., Thewissen, J.G. (eds), *Encyclopedia of Marine Mammals*, Ac. Press, San Diego, pp. 1165–1172.
- Williams, A. J. & Fuzessery, Z.M. (2010) Facilitatory mechanisms shape selectivity for the rate and direction of FM sweeps in the inferior colliculus of the pallid bat. *J. Neurophysiol.*, **104**, 1456-1471.
- Winer, J. A. & Larue, D.T. (1996) Evolution of GABAergic circuitry in the mammalian medial geniculate body. *Proc. Natl. Acad. Sci. U. S. A.*, **93**, 3083-3087.
- Wotton, J. M., Haresign, T., Ferragamo, M.J. & Simmons, J.A. (1996) Sound source elevation and external ear cues influence the discrimination of spectral notches by the big brown bat, *Eptesicus fuscus*. *J. Acoust. Soc. Am.*, **100**, 1764-1776.

Wu, C. H. & Jen, P.H. (2008) Echo frequency selectivity of duration-tuned inferior collicular neurons of the big brown bat, *Eptesicus fuscus*, determined with pulse-echo pairs. *Neuroscience*, **156**, 1028-1038.

Wursig, B. (2002) Ecology, overview. In Perrin W.F., Wursig, B., Thewissen, J.G. (eds), *Encyclopedia of Marine Mammals*, Ac. Press, San Diego, pp. 367-370.

Xiao, Z. & Suga, N. (2002) Modulation of cochlear hair cells by the auditory cortex in the mustached bat. *Nat. Neurosci.*, **5**, 57-63.

Yan, J. & Suga, N. (1996) The midbrain creates and the thalamus sharpens echo-delay tuning for the cortical representation of target-distance information in the mustached bat. *Hear. Res.*, **93**, 102-110.

Yavuzoglu, A., Schofield, B.R. & Wenstrup, J.J. (2010) Substrates of auditory frequency integration in a nucleus of the lateral lemniscus. *Neuroscience*, **169**, 906-919.